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The Proboscis of the Long-Tongued Bees: A Comparative Study[1]

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CONTENTS

ABSTRACT

The morphology and variation of the labiomaxillary complex in the long-tongued bees (families Apidae, Anthophoridae, Fideliidae, and Megachilidae) is described, including new characters, and the results applied to apoid taxonomy. Genera have been grouped by cladistic analysis into mouthpart groups, largely according to unique, shared, derived characters. This study supports a monophyletic origin for the long-tongued bees, with the Melittidae, or at least the genus *Ctenoplectra*, as a sister group. The Megachilidae are distinct from the other families. Among the Megachilidae, the Lithurginae diverge from the Megachilinae in labiomaxillary characteristics, and the Megachilini and Anthidiini are closely related, with the exception of *Dioxys*, which diverges from all other Megachilinae. Fideliids are grouped with the Anthophoridae and Apidae according to this analysis. Among the apids and anthophorids, close relationship between the Apidae and Xylocopinae is indicated, particularly between the Meliponinae and the Xylocopini. The allodapines form a distinctive group within the Xylocopinae, and elevation of these bees to tribal status may be justified. *Triepeolus* and *Thalestria* are distinct from the other Nomadinae, and reclassification of these may also be warranted. The position of *Canephorula* as a sister-group to the Eucerini is confirmed by mouthpart characteristics.

INTRODUCTION

Long-tongued bees (families Apidae, Anthophoridae, Fideliidae, and Megachilidae) have the glossa, labial palpi, and galeae as long as or longer than the stipites, and the first two segments of the labial palpi elongate, flattened, and sheathlike. Despite the functional significance and the many taxonomically useful characters of the labiomaxillary complex of bees, the morphology of and relationships indicated by bee mouthparts have been neglected in recent literature. The mouthparts of sphecoid wasps were described by Ulrich (1924), and various authors have described mouthparts of species of long-tongued bees (Michener, 1944, *Anthophora edwardsii;* Snodgrass, 1956, *Apis mellifera;* Camargo, 1967, *Melipona*

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marginata; Iuga, 1968, *Bombus terrestris, lapidarius, agrorum*). Saunders (1890), Demoll (1908), and Correia (1973) compared mouthpart morphologies for certain genera of bees, and many authors have used some characteristics of bee mouthparts for taxonomic purposes.

The purposes of the present study are: 1) to describe the morphology and variation in the labiomaxillary complex of long-tongued bees, 2) to compare characteristic features of the mouthparts of representative genera, and 3) to use characters of the mouthparts for taxonomic purposes.

MATERIALS AND METHODS

The terms labiomaxillary complex, proboscis, and mouthparts are used interchangeably in this paper to refer to the combined labium and maxillae. The mouthparts of representative genera (Table 1) were removed from specimens, cleared in 10% KOH, washed in acetic acid, and preserved for study in glycerol. Unless otherwise noted, specimens were females. Examination was with a dissecting microscope, drawings were made of distinctive structures. Other species were examined in groups whose diversity justified such work.

For comparative purposes, the classification of Michener (1944, 1974a, Table 1) is used. Since the branching sequences suggested by mouthparts are often similar to those indicated by Michener, taxonomic names are used to identify mouthpart groups. When used in the context of mouthpart group rather than a taxon, the name is followed by the word "group." All members of a taxon are not necessarily members of the same mouthpart group; such cases are discussed in the text. A similar study being conducted by L. Greenberg is the source of most of the information concerning short-tongued bees discussed here.

Genera are placed in mouthpart groups largely according to the principles of cladistic analysis, as modified by Ashlock (1974), Michener (1974b), and Mayr (1976). The mouthpart groups should not be used alone to make the classification of long-tongued bees; they are meant to show only relationships as shown by mouthparts and may or may not be identical to groupings based upon other characters. Dendrograms (Figs. 18-22) are based on mouthparts of the forms examined by me; no doubt other characters would improve them, e.g., by reducing the number of multifurcations. Synapomorphous characters (Table 2) are indicated by numbers on the stems and parenthetically in the text.

Groups lacking synapomorphous characters in the mouthparts are indicated by dotted lines in the cladograms, following the classification of Michener (1944). In the text, the terms similarity, relationship, and affinity are used interchangeably in discussing phenetic closeness. Groups not characterized by synapomorphic characters may be monophyletic, but whether they are holophyletic or paraphyletic (sense of Ashlock, 1971) cannot be determined without consideration of other characters.

Table 3 shows the morphological terms used, sources for the terms (major works on apoid structure, not relating to priority), and other terms previously used. The terminology of Michener (1944) and Snodgrass (1956) is used when it agrees with current interpretations. Terms listed without sources but with previous terminology relate to structures previously described, but renamed here. Terms with neither sources nor previous nomenclature refer to structures to the best of my knowledge not previously described or named. In the text, names of structures are italicized where they are most fully described.

The labiomaxillary complex consists of the maxillae (laterally) and labium (medially) (Fig. 1). For purposes of description, the proboscis is considered to be extended downward. Thus, "anterior" refers to the surface that is then directed forward, equivalent to "dorsal" in papers that consider the proboscis to be extended forward.

Four representative views of mouthparts (Figs. 23-45) which best reveal important structures are used: a) outer view of the maxilla, b) inner view of the maxilla, c) posterior view of the labium, and d) anterior view of the labium. Stippling indicates membranous areas; dashed lines, sclerotized regions passing behind (in the view presented) others; and dotted lines, weakly sclerotized areas. Below are listed conventions used either for clarity or because certain structures were not examined in detail for all groups.

a) Outer view of the maxilla
  1) The basistipital process is not generally shown in this view, since it is usually obscured by the cardo. It is shown in the inner view.
  2) Only the basal end of the galea is usually shown, and no galeal hairs or ribbing are included.
  3) The basal end of the suspensory thickening is not shown.
  4) Only the apical ends of basally broken cardines are shown.
  5) Only basal segments of long maxillary palpi are shown.

b) Inner view of the maxilla
  1) The galea has been unfolded to reveal the midrib and basigaleal area.

c) Posterior view of the labium
  1) Only one half of the lorum, and parts of the associated cardo and basistipital process, are shown.
  2) The glossa is represented in repose, so that the paraglossae are retracted and are not shown. The glossal rod is drawn only when visible from a posterior view; annulations and hairiness of the glossa are only sche-

TABLE 1.

List of Specimens Examined, Classified According to Michener (1944, 1974) and Winston and Michener (1977).

- Megachilidae
  - Lithurginae
    - *Lithurge gibbosus*
    - *Lithurgommia wagenknechti*
    - *Trichothurgus dubius*
  - Megachilinae
    - Anthidiini
      - *Anthidiellum notatum robertsoni*
      - *Anthidium manicatum*
      - *Aztecanthidium xochipillium*
      - *Callanthidium illustre*
      - *Dianthidium ulkei*
      - *Dioxys productus subruber*
      - *Euaspis abdominalis*
      - *Heteranthidium bequaerti*
      - *Immanthidium repetitum*
      - *Hypanthidium taboganum*
      - *Nananthidium tamaulipanum*
      - *Odontostelis bivittata*
      - *Pachyanthidium bouyssoni*
      - *Paranthidium jugatorium perpictum*
      - *Parevaspis carbonaria*
      - *Spinanthidium wolkmanni*
      - *Stelis aterrima*
    - Megachilini
      - *Anthocopa copelandica*
      - *Ashmeadiella bucconis*
      - *Chalicodoma (Chelostomoides) angelarum*
      - *Chalicodoma (Chelostomoides) exilis*
      - *Chalicodoma cincta combusta*
      - *Chalicodoma rufipes*
      - *Chalicodoma torrida*
      - *Chelostoma fuliginosum*
      - *Chelostomopsis rubifloris*
      - *Coelioxys edita*
      - *Creightonella frontalis*
      - *Heriades carinata*
      - *Hoplitis albifrons argentifrons*
      - *Megachile albitarsis*
      - *Megachile frugalis pseudofrugalis*
      - *Noteriades* sp.
      - *Osmia lignaria*
      - *Osmia subaustralis*
      - *Proteriades deserticola*
- Fideliidae
  - *Fidelia* sp.
  - *Neofidelia profuga* (male)
- Anthophoridae
  - Nomadinae
    - *Biastes brevicornis*
    - *Caenoprosopis crabronina*
    - *Holcopasites heliopsis*
    - *Leiopodus lacertinus*
    - *Nomada annulata*
    - *Thalestria* sp.
    - *Triepeolus verbesinae*
  - Anthophorinae
    - Eucerini
      - *Eucera chrysopyga*
      - *Melissodes agilis*
      - *Peponapis crassidentata*
      - *Svastra atripes*
      - *Thygater amaryllis*
      - *Xenoglossa fulva*
    - Canephorulini
      - *Canephorula apiformis*
    - Melectini
      - *Melecta californica*
      - *Thyreus ramosa*
    - Centridini
      - *Centris poecila*
      - *Epicharis elegans*
    - Anthophorini
      - *Amegilla comberi*
      - *Anthophora cockerelli*
      - *Anthophora occidentalis*
    - Tetrapediini
      - *Tetrapedia* sp. (male)
    - Exomalopsini
      - *Ancyloscelis panamensis*
      - *Caenonomada bruneri*
      - *Exomalopsis zexmeniae*
      - *Tapinotapis caerula*
    - Ctenioschelini
      - *Ericrocis lata*
      - *Mesocheira bicolor*
    - Melitomini
      - *Diadasia afflicta*
      - *Melitoma segmentaria*
  - Xylocopinae
    - Xylocopini
      - *Lestis aeratus*
      - *Xylocopa brasilianorum varipuncta*
      - *Xylocopa fimbriata*
      - *Xylocopa v. virginica*
    - Ceratinini
      - *Allodape stellarum*
      - *Braunsapis facialis*
      - *Ceratina (Ceratinidia)* sp.
      - *Ceratina (Pithitis)* sp.
      - *Ceratina calcarata*
      - *Macrogalea candida*
      - *Manuelia gayi*
- Apidae
  - Apinae
    - Apini
      - *Apis dorsata*
      - *Apis mellifera*
  - Bombinae
    - Bombini
      - *Bombus pennsylvanicus*
      - *Psithyrus variabilis*
    - Euglossini
      - *Euglossa cordata* (male)
      - *Eulaema cingulata*
      - *Eupusia* sp. (male)
      - *Euplusia violacea*
  - Meliponinae
    - *Melipona fasciata*
    - *Melipona marginata*
    - *Melipona rufiventris*
    - *Meliponula bocandei*
    - *Trigona (Hypotrigona)* sp.
    - *Trigona capitata zexmeniae*
    - *Trigona chanchamayoensis*

TABLE 2.

Synapomorphous Characters of the Mouthparts of Long-tongued Bees. See Figures 18-22 for dendrograms using these characters; the structures themselves are more fully described in the text.

1) mentum elongated and flared distally, articulating distally with the basal process of the prementum and basally with a v-shaped lorum (Figs. 1; 2c, d)
2) ligular arm distinct from prementum, with no region of continuous sclerotization between them (Fig. 14a, b)
3) basistipital process elongated
4) subligular process curved anteriorly (Fig. 13)
5) stipital comb present (Fig. 2a)
6) flabellum present at apex of glossa (Fig. 2c)
7) glossa with sclerotized rod extending its entire length
8) glossa, galea, and labial palpus as long or longer than stipes (Fig. 2)
9) galea with midrib (Fig. 2a)
10) ends of stipital sclerite not expanded (Fig. 6a)
11) stipital comb lost
12) dististipital process present (Fig. 7)
13) labial palpus with brush on cancavity of first segment (Fig. 11)
14) ligular arms ½ length of prementum or less (Fig. 14a)
15) lacinia with comb (Fig. 8c)
16) ligular arms secondarily fused with prementum (Fig. 14c)
17) inner cardinal process elongated (Fig. 3c)
18) basal process of prementum convexly curved (Fig. 10c)
19) inner and outer cardinal processes elongated (Fig. 3a)
20) subligular process separated from prementum by membranes (Fig. 12a)
21) brush on third segment of maxillary palpus (Fig. 6i)
22) expanded sclerotized region at junction of stipital and basistipital thickenings (Fig. 5e)
23) paraglossa at least ⅔ as long as glossa
24) subligular process expanded into U-shaped process (Fig. 12f)
25) paraglossa as long as glossa
26) striations in membrane underlying lacinia
27) area between subgalea and stipital sclerite partly sclerotized
28) prementum partly membranous and flattened (Fig. 12g)
29) brush on expanded lobe of the palpiger
30) bristles on membranous fold basad to the basigaleal area
31) subligular process as in Figure 12c
32) sclerotized ridge along outer margin of stipes (Fig. 4j)
33) stipital sclerite expanded apically into knob (Fig. 6d)
34) anterior longitudinal brace robust
35) both ends of stipital sclerite expanded to anterior edge of membrane lying between stipital sclerite and subgalea (Fig. 6i)
36) stipes with strong comb concavity, comb with robust, blunt teeth (Fig. 4h)
37) bipartite stipital thickening fused with stipital sclerite, with sclerotized area at junction of two sections of bipartite thickening (Fig. 5c)
38) basistipital process largely formed by expanded basistipital thickening (Fig. 5b)
39) stipital comb reduced, weak
40) bulla on inner cardinal process
41) lacinia hairless, membranous
42) transverse sclerotized ridge basal to cardinal process (Fig. 3e)
43) glossa, labial palpus, and galea much longer than stipes

matic. The apical portion of the glossa is not represented.
   3) Only the basal segment (or a part thereof) of the labial palpus is represented.
d) Anterior view of the labium
   1) Only one suspensory thickening is shown, and only its distal part.
   2) The mentum and lorum are not represented.
   3) Only one paraglossal suspensorium, paraglossa, and basal segment of the labial palpus are drawn, and one half of the basiglossal sclerite. These structures, as well as the glossa and ligular arms, are drawn in the extended position, contrary to that in the posterior view of the labium.

MORPHOLOGY OF THE LABIOMAXILLARY COMPLEX

Maxillae

The maxilla of the long-tongued bees retains the major structures of an insect maxilla (cardo, stipes, galea, lacinia, and maxillary palpus) but in modified form (Fig. 1). The cardo, stipes, and galea are elongated, and the stipes and galea are curved to sheath the labium when extended, features presumably important for nectar uptake. The

TABLE 3.

Nomenclature.

Structure	Source	Previous Terminology
Cardo	Michener (1944)	hémisternal (Iuga, 1968)
cardinal condyle	Snodgrass (1956)	....
cardinal macula	....	....
inner and outer cardinal processes	....	....
Stipes	Michener (1944)	....
stipital comb	Michener (1944)	....
comb concavity	....	....
basistipital process	....	apophyse cardinale (Iuga, 1968)
basistipital and stipital thickenings	....	....
dististipital process	....	....
stipital sclerite	....	extensory rod (Snodgrass, 1956) subgaleal sclerite (Winston and Michener, 1977)
Lacinia	Michener (1944)	....
Maxillary Palpus	Michener (1944)	....
Galea	Michener (1944)	....
blade	....	postpalpal segment of galea (Michener, 1944)
subgalea	Snodgrass (1956)	prepalpal segment of galea (Michener, 1944)
basigaleal area	....	....
lorum	Snodgrass (1956)	submentum (Michener, 1944)
Mentum	Michener (1944)	....
Prementum	Michener (1944)	sternum (Iuga, 1968)
basal process	....	....
subligular process	....	distal plate (Snodgrass, 1956) subligular plate (Michener, 1944) sternal sclerite (Iuga, 1968)
Suspensory Thickening	....	suspensory rod (Snodgrass, 1956) anterior conjunctival thickening (Michener, 1944)
Labial Palpus	Michener (1944)	....
palpiger	Michener (1944)	....
Ligular Arm	Snodgrass (1956)	héminotalia (Iuga, 1968)
Glossa	Michener (1944)	....
flabellum	Michener (1944)	....
salivary channel	Snodgrass (1956)	....
Basiglossal Sclerite	....	bonnet-shaped sclerite (Snodgrass, 1956) notal and basiglossal sclerites (Iuga, 1968)
Anterior Longitudinal Brace	Eickwort (1969)	....
Paraglossa	Michener (1944)	....
paraglossal suspensorium	....	basiparaglossa (Iuga, 1968) ligular arm (Snodgrass, 1956)

lacinia is anterior to the stipes, near the food canal, and seems to function in closing that opening when the mouthparts are retracted.

The *cardo* (Figs. 2a, d; 3) is the slender, cylindrical suspensory sclerite in the lateral wall of the otherwise membranous basal part of the proboscis; it connects the maxillae and labium to the cranium. The cardo is usually slightly curved, commonly about two thirds as long as the stipes, but as short as half the stipital length in *Xylocopa,* or as long as the stipes in many genera. The

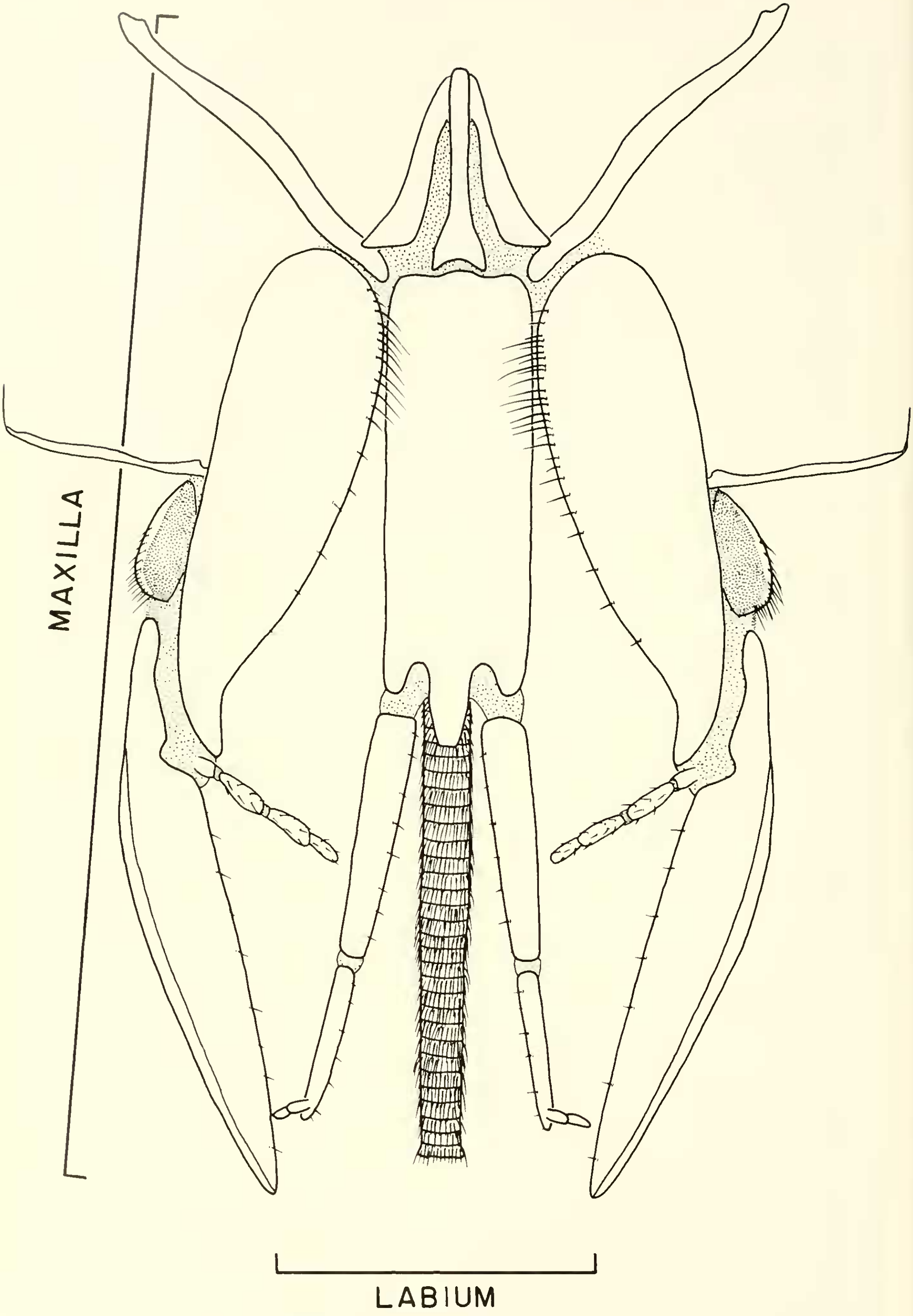


FIG. 1: Posterior view of generalized labiomaxillary complex.

cardo articulates basally with the cranium by the *cardinal condyle* (Fig. 2a); the basal terminus of the cardo extends beyond this condyle, and on this terminus is inserted the cardinal muscle, reaching to the wall of the head (Snodgrass, 1956), and the elevator muscle of the stipes, extending to the mid-region of the stipes (Iuga, 1968). In many genera, there is a cardinal macula midway along the inner surface of the cardo (Fig. 3b).

The distal end of the cardo is expanded into 2 processes, the *inner cardinal process* and the *outer cardinal process* (Figs. 2c, d; 3). The inner process curves mesad toward the mentum, perpendicular to it; the outer process curves outward toward the outer margin of the stipes. Generally one eighth to one half as long as the inner process, the outer one occasionally extends beyond the base of the stipes, forming, with the inner process, a bifurcate structure which rests upon the basistipital process (Fig. 3a) (19). The two cardinal processes connect the labium and the maxilla (Figs. 2c, d). The inner cardinal process articulates with the lorum, which is contiguous with the posterior edge of the inner process, and with the basistipital process which it overlaps. The outer cardinal process provides additional support for the cardinal-stipital articulation. In the Bombini, there is a heavily sclerotized tranverse ridge where the cardo divides into the two processes; this ridge may strengthen this area (Fig. 3e) (42). In *Apis,* there is a bulla on the inner cardinal process (Fig. 3f) (40).

The *stipes* (Figs. 2a, b; 4), a boat-shaped sclerite, extends distally along the sides of the prementum, articulating with the labium only through the cardo to the lorum, but connecting to the prementum by membrane basally. It is sclerotized on all but the inner anterior surface, forming a cavity which is closed by membranes and forms the channel in which blood and soft tissues reach the apical part of the maxilla. The stipes is two to five times as long as wide, often with a comb along the distal part of the posterior margin. The shape of the outer surface of the stipes varies considerably; some representative outer views are shown in Figure 4. The base is usually narrowed from both the anterior and posterior margins, although some genera have an expanded, antero-proximal, sclerotized flap (Fig. 4a). The apical end may be blunt (Fig. 4a), narrowed (Figs. 4c, e, f), or notched (Fig. 4g). Many genera have a sclerotized ridge medially along the outer surface of the apical third (Fig. 4j) (32).

The posterior margin of the stipes is often hairy, particularly proximally. The hairs vary in length (short, medium, long), abundance (absent, scarce, abundant, dense), and type (plumose, non-plumose, bristles) (Fig. 4). Occasionally, the anterior margin of the stipes may also be hairy, or even the entire outer stipital surface.

Most anthophorids and apids, and some megachilids (*Anthidium, Callanthidium,* and *Immanthidium*), have a *stipital comb* (Figs. 2a; 4) (5) along a well-sclerotized concave edge of the posterior distal margin of the stipes, the *comb concavity.* This concavity varies from weak (Fig. 4f) to strong (Fig. 4h), and in some species of meliponines is recessed behind the outer margin of the stipes (Fig. 4i). The bristles of the comb are generally robust, but some genera have weaker combs, with bristles attenuated distally and wide gaps between them. In *Xylocopa* and *Lestis* the bristles form extremely strong, blunt teeth (Fig. 4h) (36). Generally, stronger concavities contain stronger bristles. Some of the long-tongued bees without combs retain the comb concavity, occasionally with hairs in place of the comb. The stipital comb functions in cleaning and pollen manipulation (Schremmer, 1972; Jander, 1976).

The *basistipital process* (Figs. 2b, c, d; 5) is at the proximal end of the stipes. Despite its importance in the cardinal-stipital articulation, it has been neglected in the literature; only Iuga (1968) mentions it as the "apophyse cardinale." I have renamed it since it is an extension of the stipes. It is formed by merged proximal extensions of the base of the outer margin and the sclerotized inner anterior edge of the stipes, the basistipital thickening. The basistipital proc-

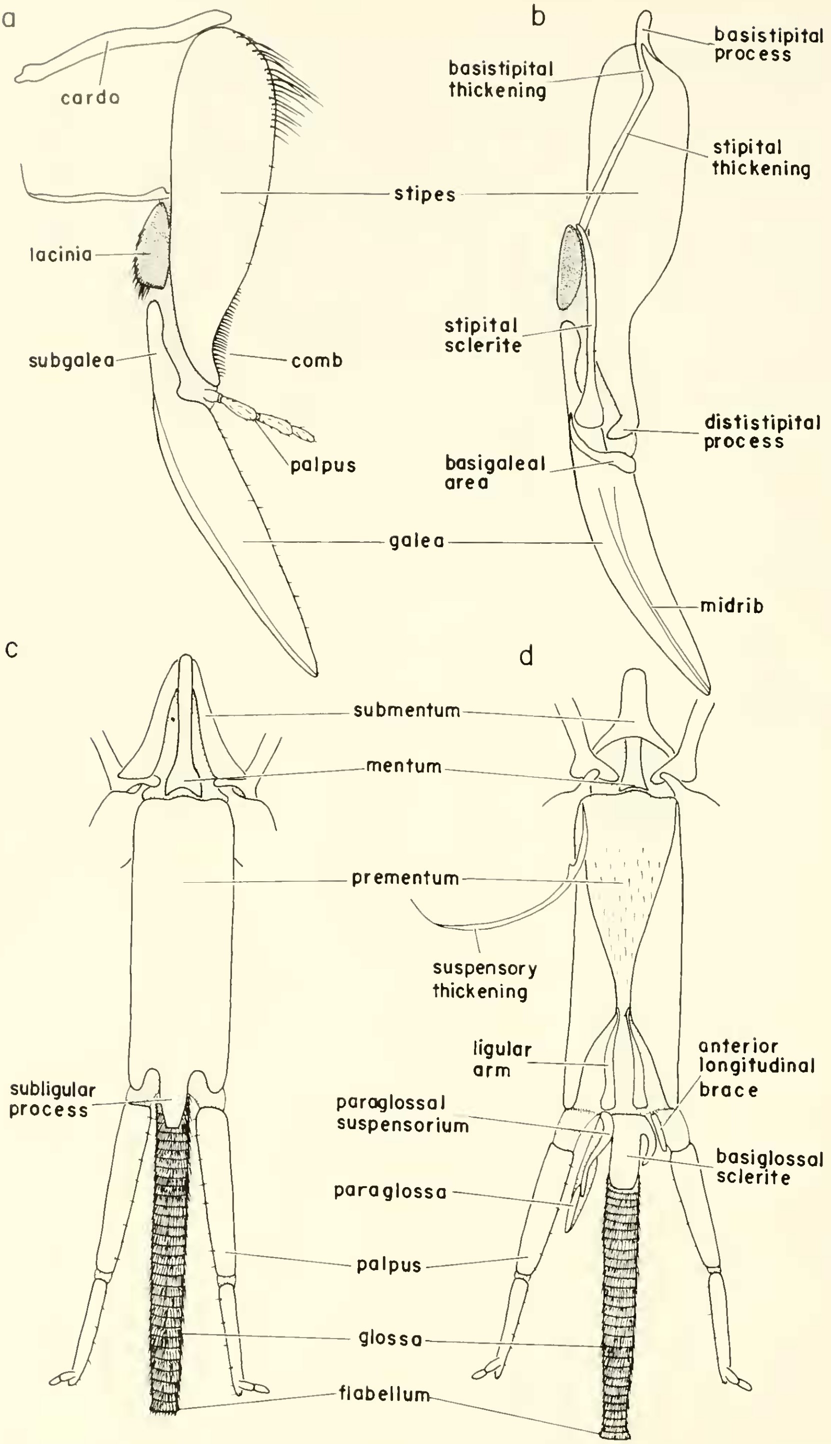


Fig. 2: Representative views of generalized labiomaxillary complex, showing nomenclature of structures. a) outer view of the maxilla, b) inner view of the maxilla, c) posterior view of the labium, d) anterior view of the labium.

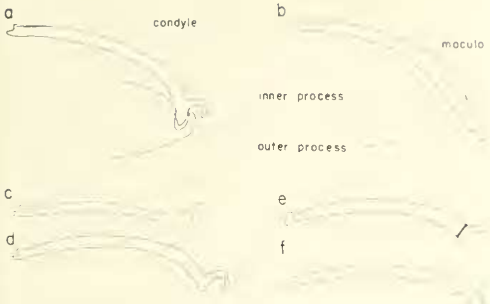


FIG. 3: Cardines of selected genera. a) *Neofidelia*, b) *Anthophora*, c) *Holcopasites*, d) *Caenonomada*, e) *Bombus*, f) *Apis*.

ess extends mesad and curves under the inner cardinal process, being mostly obscured in an outer view of the stipes. In some genera it extends beyond the inner cardinal process, and abuts against the inner edge of the lorum. In many meliponines, the basistipital process is separated from the outer margin of the stipes, and is formed largely by the extension of the basistipital thickening (38). It is also expanded apically as a distinct sclerotized pad which abuts against the lorum (Fig. 5b). It is similar to this in the Bombini, but partly formed by the outer margin of the stipes. Membranes loosely connect the basistipital process and the inner cardinal process, allowing free longitudinal movement of the maxilla and, through the articulation between the cardo and the lorum, of the labium as well.

Basally the inner surface of the stipes is narrower than the outer surface so that, in an inner view, the anterior part of the outer stipital wall can be seen (Fig. 2b). The anterior edge of the inner surface is thickened basally, forming the well sclerotized *basistipital* and *stipital thickenings* (Figs. 2b; 5). The basistipital thickening forms and reinforces the posterior edge of the basistipital process. The stipital thickening extends from the distal end of the basistipital thickening to a point midway along the stipes and is one to three times as long as the basistipital thickening. In *Thalestria* and *Triepeolus* the two thickenings meet at an expanded sclerotized area (Fig. 5e) (22). Apically, the stipital thickening extends beyond the edge of the body of the stipes (Fig. 2b), abutting against the proximal end of the stipital sclerite and fusing with it in many genera (Fig. 5c, d). While the stipital thickening is usually straight or smoothly curved (Fig. 2b), it sometimes has two sections (referred to here as bipartite), as in the Xylocopinae and some Apidae (Fig. 5c) (37). The sclerotization of the stipital thickening probably strengthens the connection between the stipes and the stipital sclerite.

The *stipital sclerite* (Figs. 2b; 6) is a slender sclerite on the inner side of the maxilla close to the inner edge of the stipes, extending from the basigaleal area to the distal end of the stipital thickening. Usually curved, it is separable from the stipes in all but *Xylocopa brasilianorum* and *X. fimbriata*, in which it is well-attached to the inner anterior edge of the stipes and overlapped by membranes (Fig. 38). The suspensory thickening is connected by membranes to the proximal end of the stipital sclerite and links the prementum and maxilla. In many genera, either the apical end or proximal end of the stipital sclerite, or both, are expanded as triangular or rounded

FIG. 4: Stipites of selected genera. a) *Eucera*, b) *Chalicodoma*, c) *Stelis*, d) *Anthophora*, e) *Mesocheira*, f) *Tetrapedia*, g) *Neofidelia*, h) *Xylocopa*, i) *Melipona*, j) *Exomalopsis*, k) *Anthidiellum*.

processes (Fig. 6) (33, 35). An oval membranous area connects the subgalea, stipital sclerite, and the lacinia; in some anthophorids, it is partly sclerotized (27). Snodgrass (1956) calls the stipital sclerite the extensory rod, and it presumably is involved in movements of the lacinia and the galea. It has also been called the subgaleal sclerite by Winston and Michener (1977), who thought it to be derived from the inner edge of the subgalea, but L. Greenberg (in prep.) shows it to be fused with the stipes in sphecoid wasps and many short-tongued bees, suggesting a derivation from the inner distal margin of the stipes.

All megachilids except *Dioxys* have a *dististipital process* (Figs. 2b; 7) (12) perpendicular to the distal end of the stipes, extending anteriorly. It is a short distal bulge in some genera (Fig. 7a); in others it extends across the galeal-subgaleal junction toward the anterior edge of the galea (Fig. 7b). Its function is not clear. Since the galeal-subgaleal junction rests upon it, it may help to move the galea, perhaps as a rod against which the galea can be pulled into the folded resting position.

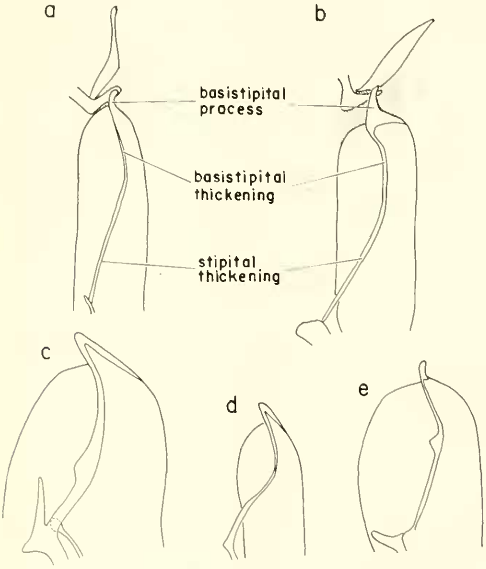


FIG. 5: The basistipital process and stipital and basistipital thickenings of selected genera. a) *Dioxys,* b) *Melipona,* c) *Xylocopa,* d) *Nomada,* e) *Triepeolus.*

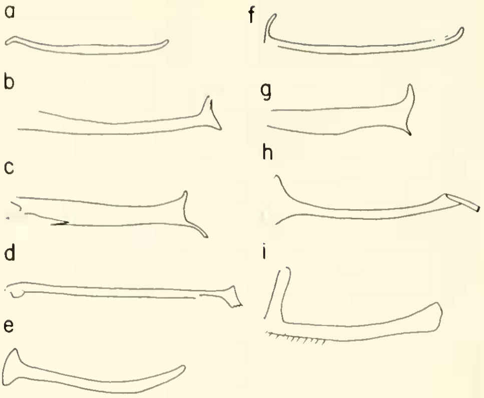
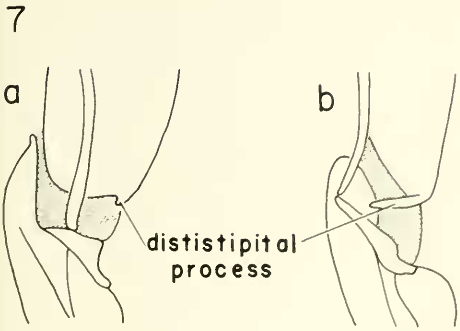


FIG. 6: Stipital sclerites of selected genera. a) *Megachile,* b) *Euplusia,* c) *Apis,* d) *Ceratina,* e) *Tetrapedia,* f) *Diadasia,* g) *Anthophora,* h) *Bombus,* i) *Melipona.*

The *lacinia* (Figs. 2a, b; 8) is a partly sclerotized or sometimes membranous lobe midway along the anterior edge of the stipes, basal and mesal to the subgalea. Membranes connect its base to the base of the stipital sclerite and to the suspensory thickening, which passes immediately basal to the lacinia. Its anterior edge is usually well-sclerotized (Figs. 8a, b), with sclerotization sometimes extending posteriorly along the distal edge as well (Figs. 8c, d). The regions supporting the sclerotized edges of the lacinia are membranous; in *Apis,* the entire lacinia is membranous (Fig. 8e) (41). In most anthidiines and in *Coelioxys,* there is a lacinial comb along the distal (and sometimes anterior) edge, made up of straight, relatively robust bristles (Figs. 8c, d) (15). In other genera the anterior sclerotized areas of the laciniae are unusually hairy, the hairs ranging from sparse (Fig. 8f) to abundant (Fig. 8a). Some genera (such as *Apis,* Fig. 8e) lack all lacinial hairs (41).

The *maxillary palpus* (Figs. 2a, b) of 1-6 segments arises from a membranous area immediately distal to the apex of the stipes. The basal segment is generally broader than the distal ones. The palpus is often hairy, occasionally with bristles. There is a brush on the third segment in *Melitoma* and *Diadasia* (Figs. 11b; 43) (21).

The *galea* (Figs. 2a, b) is a long, thin, tapering blade, convex on the outer surface and concave on the inner, posterior surface. It arises from the distal end of the stipes,



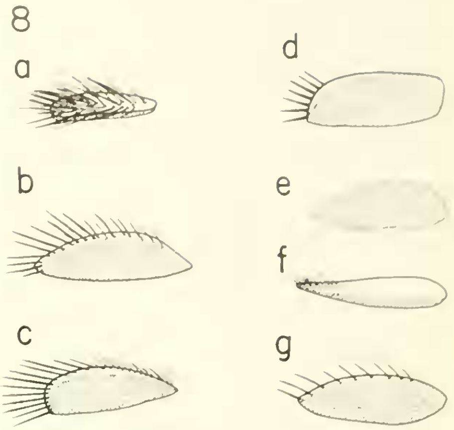


FIG. 7: *Dististipital process of selected* genera. a) *Lithurge*, b) *Hypanthidium*.

FIG. 8: Laciniae of selected genera. a) *Xylocopa*, b) *Stelis*, c) *Hypanthidium*, d) *Coelioxys*, e) *Apis*, f) *Osmia*, g) *Hoplitis*.

and is divided into two regions, the postpalpal *blade* and the much shorter, prepalpal, triangular *subgalea* (Fig. 2a). Between the galeal blade and the subgalea, where the galea bends backwards in repose, the galea is narrowed. This narrowed region is strengthened on the inner, concave surface by the *basigaleal area* (Figs. 2b; 9), a region of heavier sclerotization generally extending along the basal edge of the blade, more or less transverse to the main axis of the galea. A prominent *midrib* extends the length of the blade (9), as a fold in the inner galeal wall, often supported basally by the anterior edge of the basigaleal area. Hairs often arise from the midrib, sometimes extending to the edge of the galea. The blade is well-sclerotized basally, often less so distally. The distal area of lighter sclerotization often appears ribbed, probably due to channels through the sclerotic material that connect hairs on the edges of the galea to the region of the midrib.

Labium

The labium of long-tongued bees can be divided transversely into three regions, the postmentum, prementum, and ligula (glossa, paraglossa, and labial palpus) (Fig. 1). The prementum is between the stipites; the glossa, paraglossa, labial palpus, and associated sclerites are articulated at its apex. The sclerites of the postmentum (lorum and mentum) connect the base of the prementum to the maxillae. Michener (1944) noted misinterpretations which confused the mentum with the submentum, and the prementum with the mentum. As there is either one or no postmental plate in other Hymenoptera (Kirkmayer, 1909; Duncan, 1939), the lorum may be a secondarily derived structure not homologous with the primitive insect submentum. I use the term mentum to designate the distal sclerite of the postmentum.

The proximal sclerite of the postmentum, the lorum (submentum of some authors) is v-shaped, with its divergent arms articulated to the distal ends of the maxillary cardines as previously described (Figs. 2c, d). Its medial region articulates with the distal sclerite of the postmentum, the *mentum*, the proximal end of which curves over the lorum (Figs. 2c, d). The mentum is elongate, thin, and flared distally where it connects with the prementum. The distal margin of the apical expansion of the mentum may be slightly concave (Fig. 10a), concave (Fig. 10b), bifurcated (Fig. 10c), notched (Fig. 10d), or reduced (Fig. 10e), and articulates with the base of the prementum (Figs. 2c; 10). The connections of the lorum to the maxillary cardines and the prementum through the mentum, allow the labiomaxillary complex to be protracted and retracted as a single unit. At least in *Apis*, the protractor muscles insert on the maxillae, the retractor muscles on the labium, so that movements of the maxillae and the labium are completely interdependent (Snodgrass, 1956).

The labiomaxillary complex is strengthened basally by the *suspensory thickenings* (Figs. 2a, d), a pair of ribbon-like bands in the anterior conjunctiva of the proboscis (the anterior conjunctival thickenings of Michener, 1944). The distal end of each thickening connects to the anterior surface of the prementum near the base. From there it extends to the inner edge of the lacinia, then curves anteriorly, supporting the conjunctiva, passing lateral to the mouth before turning toward the paramandibular process of the hypostoma (Michener, 1944). The sclerotization of the suspensory thickening is often expanded where it curves anteriorly; this expanded area may represent the fusion of the two segments of the suspensory thickening present in short-tongued bees (except Melittidae, R. McGinley, pers. comm.). Membrane connects this area to the lacinial-stipital junction, further linking the labium with the maxillae.

The *prementum* (Figs. 2c, d) is an elongated sclerite, usually slightly wider distally than proximally, located between the two stipites. It is convex posteriorly and concave anteriorly, the concavity being closed by membrane, continuous with the labiomaxillary tube, and containing the muscles of the glossa and paraglossae (Michener, 1944). The articulation with the mentum is by means of the basal process of the prementum (Fig. 10), a usually concave expansion of the base of the prementum. In some genera the base is convex (Fig. 10c) (18) or reduced (Fig. 10e). Distally, the posterior premental surface is trilobed, the outer lobes contiguous with the labial palpi, the central lobe forming the subligular process. In *Canephorula*, the prementum is partly membranous (Fig. 12g) (28).

The *labial palpus* (Figs. 2c, d) articulates with the outer apical lobe of the prementum through the largely membranous *palpiger* (Fig. 2c), which sometimes is strengthened by a narrow longitudinal sclerotic slip. The

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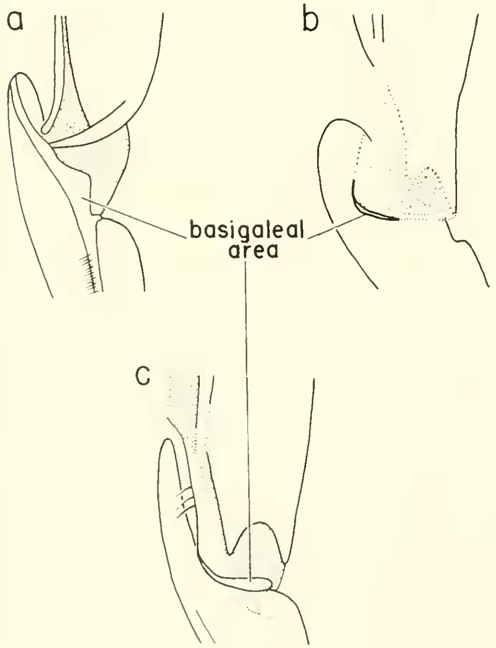

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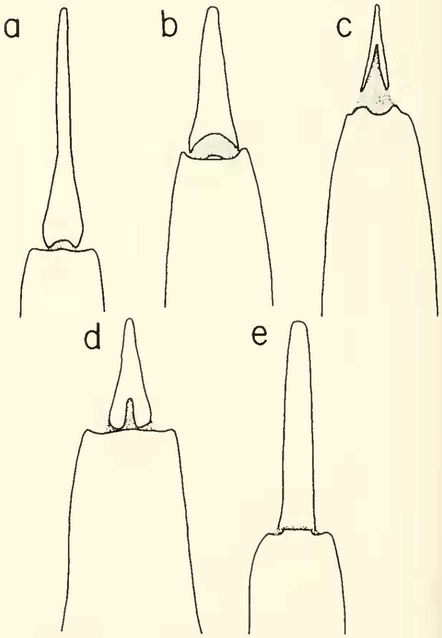

FIG. 9: Basigaleal area of selected genera. a) *Heteranthidium*, b) *Triepeolus*, c) *Melecta*.

FIG. 10: Menta of selected genera, showing variation in distal end. a) *Eucera*, slightly concave, b) *Dioxys*, concave, c) *Nomada*, bifurcate, d) *Lithurge*, notched, e) *Exomalopsis*, reduced.

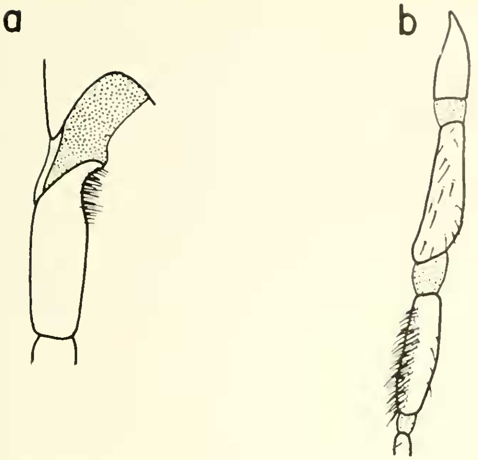

Fig. 11: a) Brush on first labial palpal segment of *Lithurge*, b) Brush on third maxillary palpal segment of *Diadasia*.

palpus consists of four segments separated by membranes. The two basal segments are elongate, flattened, and concave on the inner surfaces so as to sheath the glossa. These two segments are well sclerotized medially, with lighter sclerotization along the lateral margins. The relative lengths of the basal segments vary. The two distal subcylindrical segments arise subapically on the second segment, and project almost perpendicularly to it. The labial palpus is often hairy, sometimes bristly. The Lithurginae have a brush on a concavity of the proximal inner edge of the first segment (Fig. 11a) (13). There is a small brush on an expanded, sclerotized lobe of the palpiger in *Melecta* and *Thyreus* (Fig. 33) (29).

The base of the glossa is supported posteriorly by the *subligular process* (Figs. 2c; 12), which extends distally from the apex of the prementum, curving anteriorly at its apex, perpendicular to the glossa (Fig. 13) (4). In the *Anthophora* group, it extends to form a u-shaped process upon which the glossa rests (Fig. 12f) (24). In a few genera the subligular process is separated from the apex of the prementum by a narrow membranous area (Fig. 12a) (20). Fig. 12 shows representative configurations of the subligular process.

On the anterior surface of the prementum, the two *ligular arms* (Figs. 2d; 14) are located lateral to the base of the glossa. Each is a narrow sclerite, slightly expanded apically, extending from midway along the prementum almost to its apex, except in the Lithurginae, where the ligular arm extends nearly to the base of the prementum (Fig. 14b). Each incurved lateral margin of the prementum (or premental fold) has a region of expanded sclerotization at the base of the ligular arm; in the Apidae, Anthophoridae, and Fideliidae, the base of the ligular arm merges with this sclerotized area (Fig. 14c) (16). In the Megachilidae, the ligular thickening is not continuous basally with the sides of the prementum, but is the concave anterior surface of the prementum, connected to the sides of the prementum by membranes (Fig. 14a). When the glossa is retracted, its base rests between the ligular arms. When protracted, the base of the

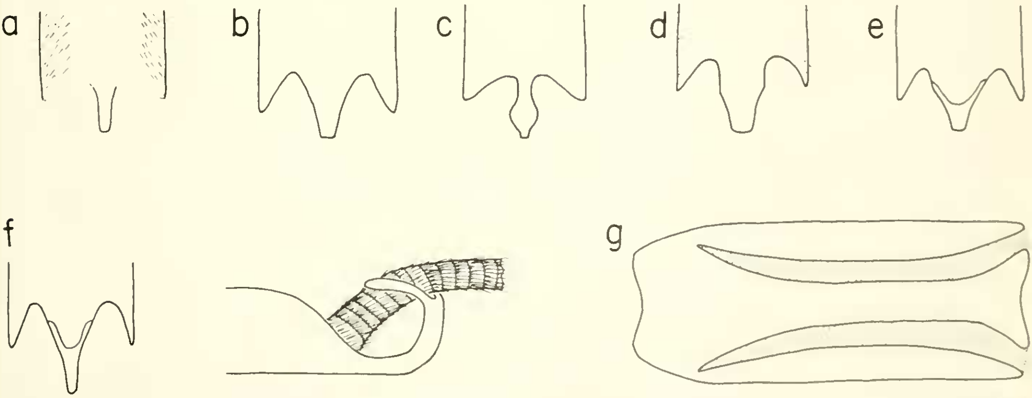

Fig. 12: Subligular processes of selected genera. a) *Neofidelia*, b) *Svastra*, c) *Tetrapedia*, d) *Holcopasites*, e) *Exomalopsis*, f) *Anthophora* (with lateral view), g) *Canephorula* (whole prementum).

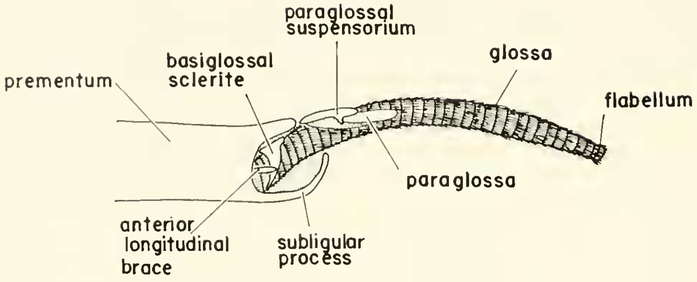

FIG. 13: Lateral view of generalized ligular region and glossa.

glossa extends beyond the apices of the ligular arms. In Megachilidae the ligular arms can move slightly in the same direction as the glossa; this mobility may increase the distance that the glossa can be protracted.

The *glossa* (Figs. 2c, d; 13), arises at the apex of the prementum, as a fusion product of the primitive, paired glossae (Snodgrass, 1956; Michener, 1944). It is usually slightly longer than the prementum, and densely hairy, split posteriorly by a longitudinal medial groove, the *salivary channel* (Snodgrass, 1956). A flexible rod extends the length of the inner wall of the salivary channel (7), although it is often only apparent in a cross-section. Transverse rows of setae alternate with bare areas, giving the glossa a ringed appearance. At its apex the glossa is expanded into the flabellum (Fig. 2c) (6). (Since a systematic study of glossal cross-sections was not done, variation in the salivary channel, rod, and flabellum is not a part of this study). In the euglossines, the glossa is greatly elongated (as are the labial palpi and the galea), sometimes extending well beyond the tip of the abdomen (43).

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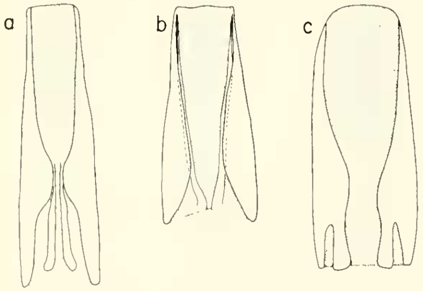

FIG. 14: Ligular arms of selected genera, showing three major types. a) *Stelis* (short, distinct from prementum), b) *Lithurge* (elongate, not fused with prementum), c) *Apis* (short, fused with prementum).

The *basiglossal sclerite* (bonnet-shaped sclerite, Snodgrass, 1956; notal and basiglossal sclerites, Iuga, 1968) (Figs. 2d; 15) partly encloses the base of the glossa antero-laterally. Laterally, it forms two thin processes extending posteriorly that appear like the tie strings of a bonnet. Lateral to the basiglossal sclerite, on the inner side of the paraglossal suspensorium, are two short sclerites, the *anterior longitudinal braces* (Fig. 13), present in many but not all genera.

Lateral to the glossa are the two *paraglossae,* elongate lobes each arising on a paraglossal suspensorium at the base of the glossa (Figs. 2c; 13; 16). The paraglossa varies from mostly sclerotized to mostly membranous, commonly largely membranous, often concave mesally and fitting snugly against the posterior glossal surface. Usually less than one quarter the length of the glossa, in some genera (Eucerini, Melectini, *Canephorula*) paraglossae extend the length of the glossa (23, 25). They are occasionally hairy.

The *paraglossal suspensorium* (basiparaglossa of Iuga, 1968), a sclerotized base for the paraglossa lateral to the base of the glossa, has a posteriorly directed arm upon which the paraglossa arises. In the Xylocopinae, Apidae, and some Exomalopsini, the paraglossa is broadly attached to the paraglossal suspensorium (Fig. 16a), while in other genera the articulation is narrow (Fig. 16b). Snodgrass (1956) considered the paraglossa to arise from an apical extension of the ligular arm, thinking that the paraglossal suspensorium was part of the ligular arm. However, when the proboscis is protracted, the paraglossal suspensorium and the paraglossa move with the glossa, while the ligular arm remains stationary; thus the paraglossal suspensorium is clearly a separate sclerite. At rest, the base of the glossa, the paraglossae, and the paraglossal suspensoria lie between the ligular arms.

Movement of the Labiomaxillary Complex

The protraction and retraction of the labiomaxillary complex has been described for *Anthophora edwardsii* (Michener, 1944) and *Apis mellifera* (Snodgrass, 1956). When at rest, the proboscis is folded below the head, in three sections, in a z-shaped pattern. The basal section, containing cardines, lorum, and mentum, is directed posteriorly, and articulates with the head through the cardinal condyles. The midsection, made up of the stipites and prementum, folds anterior beneath the cardines. The third section (glossa, paraglossae, labial palpi, and galeae) rests beneath the stipites and prementum and folds posteriorly towards the neck.

As mentioned above, retraction and protraction in *Apis* depends on maxillary protractor muscles and labial retractor muscles, the proboscis rocking in and out on the articulations of the cardines with the head. When extended, the glossal section bends anteriorly until almost in line with the stipites and prementum, while the cardines, mentum, and lorum move forward until they are below the maxillary processes of the head. The galeae and labial palpi support the distal part of the glossa, while the basiglossal sclerite, ligular arms, subligular process, paraglossáe, and paraglossal suspensoria support the base. Snodgrass (1956) describes the sucking action of the proboscis.

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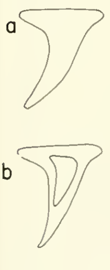

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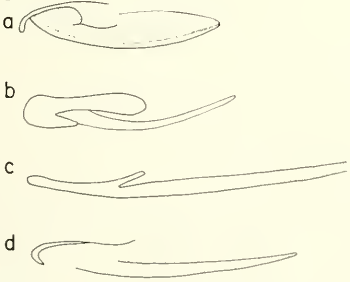

Fig. 15: Basiglossal sclerites of selected genera. a) *Melipona*, b) *Anthidium*.

Fig. 16: Lateral views of the paraglossa and paraglossal suspensorium of selected genera. a) *Exomalopsis* (broadly attached), b) *Centris* (not broadly attached), c) *Thygater*, d) *Thyreus*.

COMPARATIVE STUDY

Long-tongued bees are distinguished from short-tongued bees by many characters. (The following discussion excludes the short-tongued bee *Ctenoplectra;* see below.) The prementum, glossa, first two segments of the labial palpus, and galea of long-tongued bees are longer relative to other mouthpart structures than in short-tongued bees (8). Although some short-tongued bees have an elongated glossa (e.g., *Thrinchostoma*), or elongated prementum and stipites (e.g., many halictines), there are no species with the combination of elongated labiomaxillary structures listed above. In long-tongued bees, the lorum is V-shaped and the mentum is elongated and narrow, especially basally (1). In short-tongued bees, the lorum is not V-shaped, but is broad (except in the melittids, where lorum and mentum closely resemble those of the long-tongued bees), or reduced or absent in some halictids. The mentum (again with the exception of melittids) is relatively short, and generally broader than in long-tongued bees, or is sometimes more or less membranous or absent.

Other distinguishing structures of long-tongued bees are important in the support and function of the elongate proboscis. The glossa has a terminal flabellum (6) and an internal sclerotized rod (7), both absent in the short-tongued bees. Other characters not found in the short-tongued bees are the anterior curving of the subligular process (4), which could act to support the glossa, and the presence of the galeal midrib

(9), important in strengthening the galea which sheathes the extended glossa. The sclerotized ridge on the inner surface of the galea in some short-tongued bees may be homologous with the galeal midrib of the long-tongued bees.

The two groups of bees also differ in the location of maxillary combs. Short-tongued bees often have a comb on a sclerotized plate of the inner galeal wall (Fig. 17), perhaps corresponding to the galeal comb of sphecoid wasps. This plate is probably homologous with the basigaleal area of long-tongued bees (Figs. 2b; 9). However, long-tongued bees have no galeal comb, although Jander (1976) suggests that rudiments of a galeal comb may be present in *Ceratina* (none has been found in this study). Many genera of long-tongued bees do have a comb on the posterior edge of the distal part of the stipes (Fig. 2a) (5), absent in all short-tongued bees except *Ctenoplectra* (Melittidae). Jander (1976) suggests that the galeal and stipital combs are equifunctional, involved in cleaning movements of the foreleg, homologous to similar cleaning movements of most other Hymenoptera.

Many other characteristics of certain groups of long-tongued bees appear to be derived from more primitive, short-tongued ancestors. The inner and outer cardinal processes of short-tongued bees, as well as the basistipital process, are usually short; their elongation in some long-tongued genera is probably derived. The stipital sclerite of short-tongued bees is variable, but usually expanded basally, apically, or both; reduction of these expansions presumably also is a derived condition. Moreover, short-tongued bees have no dististipital process, lacinial

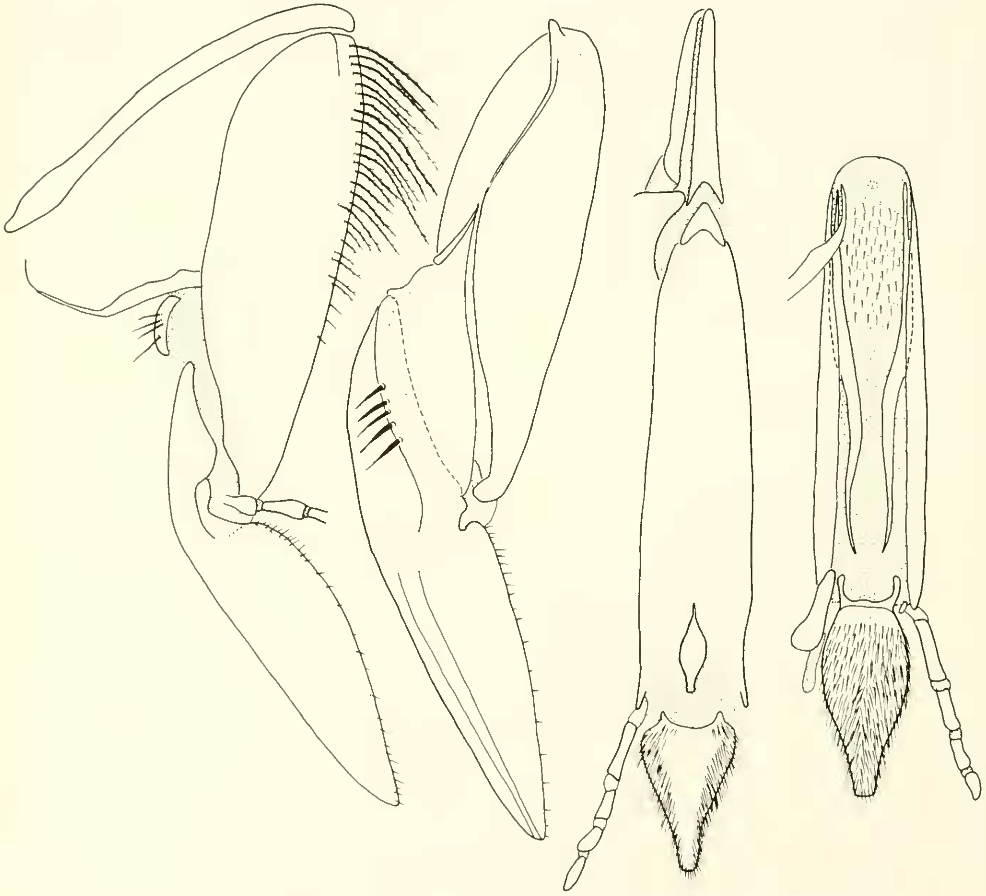

Fig. 17: Labiomaxillary complex of the short-tongued bee *Melitta leporina* (Melittidae).

comb, notched mentum, or brush on the labial palpus, all characters of some groups of long-tongued bees.

Ctenoplectra, which has been classified with the short-tongued family Melittidae, and is indeed a short-tongued bee, has been largely excluded from the above discussion since it has certain characteristics of long-tongued bees (L. Greenberg, pers. comm.). *Ctenoplectra* lacks a galeal comb, and unlike all other short-tongued bees, has a stipital comb similar to that of many long-tongued bees. Other characters common to long-tongued bees and *Ctenoplectra,* but absent in other short-tongued bees, include a flabellum, sclerotized glossal rod, and an anteriorly curved subligular process. Like other melittids, its mentum and lorum, as well as the articulation between the mentum and prementum, are like those of long-tongued bees. The length of the glossa, galea, and labial palpus of *Ctenoplectra* are similar to those of other short-tongued bees.

Long-tongued bees can be divided into two mouthpart groups, with the Megachilidae in one and Apidae, Anthophoridae, and Fideliidae in the other, here called the anthophoroid group (Fig. 18). The Megachilidae are characterized by a dististipital process (Fig. 7) (12), a thin stipital sclerite without expanded ends (Fig. 6a) (10), and a ligular arm which is not continuous with the prementum (Fig. 14); the first two characters are synapomorphous for the Megachilidae. Also, the lacinia is either curved, with a comb (Fig. 8c), or elongated, without a comb (Fig. 8f), and the stipital comb is absent in all genera except *Anthidium, Callanthidium,* and *Immanthidium* (11). In the anthophoroid group, on the other hand, the dististipital process is absent, the stipital comb is often present (Figs. 4a, d, e, f, h, i, j), the lacinia is variable, never with a comb (Figs. 8a, e), the stipital sclerite is generally expanded at one or both ends (Figs. 6b, c, e-i), and the ligular arm is fused with the prementum (Fig. 14c) (16). The last character is synapomorphous for the anthophoroid group. Since most short-tongued bees except *Melitta* and *Ctenoplectra* have fused ligular arms, this character is likely to be secondarily derived in the anthophoroid line.

Megachilidae

Within Megachilidae, Lithurginae (Fig. 23) form a distinctive group, many characters differentiating it from the other megachilids (Megachilinae and *Dioxys*) (Fig. 18, a dendrogram based on megachilid mouthparts; Table 4, a list of genera in each group). The lithurgine labial palpus has a brush at the base of the first segment, in a concavity of the inner surface, composed of long but not particularly stiff hairs (Fig. 11a) (13). The ligular arm extends nearly to the base of the prementum, adjacent to the distal end of the suspensory thickening (Fig. 14b), and is not as freely movable as the shorter ligular arm of the other megachilids (14). Also, the mentum of lithurgines is notched (Fig. 10d). Other characters uniting the Lithurginae but not unique to them include similar stipital shape (like Fig. 4g), the elongated basistipital process reaching to the lorum, short dististipital process (Fig. 7a), and similarly shaped basiglossal sclerite, paraglossal suspensorium, and paraglossa.

Dioxys (Fig. 24) is grouped with the Megachilinae because of its free ligular arm (Fig. 14a), lack of a stipital comb, and simple stipital sclerite (as Fig. 6a). However, it is unique among the megachilids in lacking the dististipital process and in having a reduced lacinia, and so is placed as a separate group. *Dioxys* also has a hairy outer surface of the stipes and a one-segmented maxillary palpus. It resembles the Megachilinae more than the Lithurginae in other characters, suggesting closer affinity with the former.

The tribes Anthidiini and Megachilini in the Megachilinae differ primarily in lacinial shape, the lacinia of anthidiines being usually curved, with a comb (Fig. 8c) (15) (except the *Stelis* group, see below). Some Megachilini, however, have the lacinia only slightly less curved, although without a comb (*Hoplitis* and *Chelostomopsis,* Fig. 8g). Other characteristics which recur in some but not all genera of both tribes include

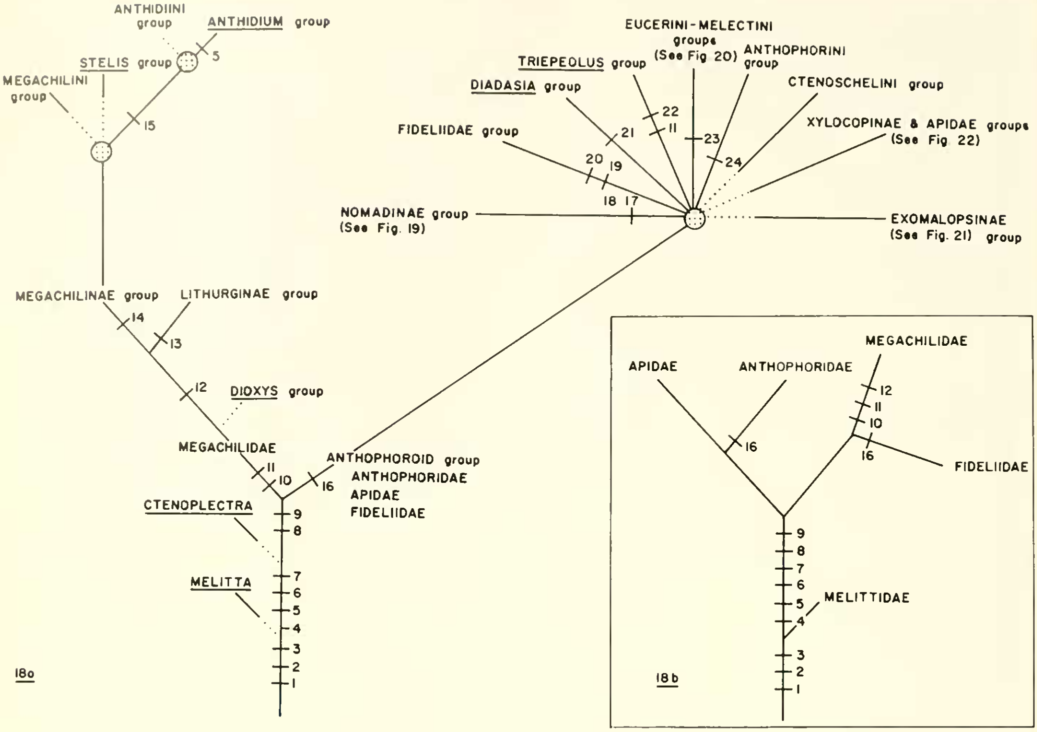

FIG. 18: a) Dendrogram showing relationships among proboscides of long-tongued bees. b) Higher classification according to Michener (1974). Dotted lines indicate groups for which there are no synapomorphic characters.

extension of the basistipital process to the lorum, plumose hairs on the stipes, long dististipital process, bifurcated mentum, similarly shaped subligular process, hairy labial palpus, and shape and relative lengths of the paraglossa and associated sclerites. While the lacinial morphology suggests divergence of the two tribes, similarities between them point to close relationship; on the basis of mouthparts alone these tribes would not be separated.

Except for the *Stelis* group and the *Anthidium* group (see below), Anthidiini are remarkably similar (Figs. 25, 26). The cardo is often widened centrally, and the stipes is generally slightly convex posteriorly, flattened anteriorly, with long bristles or plumose hairs along the posterior basal margin. The maxillary palpus is two- to three-segmented and the lacinia is curved, usually with a comb along the anterior margin (Fig. 8c). The dististipital process reaches to or almost to the stipital sclerite (Fig. 7b). The basigaleal area extends beyond the apex of the stipital sclerite (Fig. 9a). The subligular process is broad at the base, and the ligular arm, paraglossal suspensorium, and paraglossa are usually equal in length, although the length of the paraglossa may vary. The only exceptional variations among anthidiines are presence of a stipital comb in *Anthidium*, *Callanthidium*, and *Immanthidium* (Fig. 28) (structures unique to these genera among the megachilids), and lack of a lacinial comb in the *Stelis* group (Figs. 8b, 27). These genera are otherwise similar to other anthidiines, and both of these characters are likely to be secondarily derived.

The Megachilini (Fig. 29) form a fairly uniform group, without distinctive subgroups. There are no synapomorphous characters which distinguish Megachilini, nor are there such characters which might indicate the branching pattern within the megachilines. Only lacinial morphology of megachilines allows distinction from anthidiines. Generally, the maxillary palpus of megachilines has more segments (3-5) than that of

TABLE 4.

GENERA INCLUDED IN EACH MOUTHPART GROUP.

- DIOXYS GROUP
  - *Dioxys*
- LITHURGINAE GROUP
  - *Lithurge*
  - *Trichothurgus*
  - *Lithurgommia*
- MEGACHILINI GROUP
  - *Chalicodoma*
  - *Hoplitis*
  - *Chelostomopsis*
  - *Proteriades*
  - *Ashmeadiella*
  - *Creightonella*
  - *Chelostoma*
  - *Osmia*
  - *Anthocopa*
  - *Megachile*
  - *Noteriades*
- ANTHIDIINI GROUP
  - *Heteranthidium*
  - *Spinanthidium*
  - *Dianthidium*
  - *Paranthidium*
  - *Coelioxys*
  - *Hypanthidium*
  - *Aztecanthidium*
  - *Nananthidium*
  - *Anthidiellum*
  - *Pachyanthidium*
  - *Notanthidium*
- ANTHIDIUM GROUP
  - *Anthidium*
  - *Callanthidium*
  - *Immanthidium*
- STELIS GROUP
  - *Stelis*
  - *Odontostelis*
  - *Euaspis*
  - *Parevaspis*
- NOMADINAE GROUP
  - *Leiopodus*
  - *Caenoprosopis*
  - *Nomada*
  - *Holocopasites*
  - *Biastes*
- FIDELIIDAE GROUP
  - *Fidelia*
  - *Neofidelia*
- DIADASIA GROUP
  - *Diadasia*
  - *Melitoma*
- TRIEPEOLUS GROUP
  - *Triepeolus*
  - *Thalestria*
- EUCERINI GROUP
  - *Thygater*
  - *Svastra*
  - *Peponapis*
  - *Eucera*
  - *Xenoglossa*
  - *Melissodes*
- CANEPHORULA GROUP
  - *Canephorula*
- MELECTINI GROUP
  - *Melecta*
  - *Thyreus*
- ANTHOPHORINI GROUP
  - *Anthophora*
  - *Centris*
  - *Amegilla*
  - *Epicharis*
- CTENOSCHELINI GROUP
  - *Mesocheira*
  - *Ericrocis*
- ALLODAPINE GROUP
  - *Allodape*
  - *Braunsapis*
  - *Macrogalea*
- CERATININI GROUP
  - *Ceratina*
  - *Manuelia*
- XYLOCOPINI GROUP
  - *Xylocopa*
  - *Lestis*
- MELIPONINAE GROUP
  - *Melipona*
  - *Trigona*
  - *Hypotrigona*
  - *Meliponula*
- APINAE GROUP
  - *Apis*
- BOMBINI GROUP
  - *Bombus*
  - *Psithyrus*
- EUGLOSSINI GROUP
  - *Euglossa*
  - *Euplusia*
  - *Eulaema*
- EXOMALOPSINI GROUP
  - *Exomalopsis*
  - *Ancyloscelis*
  - *Tapinotapis*
  - *Caenonomada*
- TETRAPEDIA GROUP
  - *Tetrapedia*

anthidiines (1-3), and the ligular arm is often slightly longer (from one to one and a half times the length of the paraglossal suspensorium), but these characters do not differentiate the two tribes. For example, there exist megachilines with two-segmented maxillary palpi (certain species of *Ashmeadiella*) and anthidiines with five-segmented maxillary palpi (*Trachusa*).

Anthophoroid group

The anthophoroid mouthpart group (families Apidae, Fideliidae, and Anthophoridae) is much more diverse at tribal and generic levels than is the Megachilidae. Certain characters are particularly useful in indicating the branching sequences throughout the group, e.g., shapes of the stipital sclerite and cardinal processes, lengths and shapes of the paraglossa and paraglossal suspensorium, and shape of the subligular process. (Figures 18 to 22 are dendrograms of the anthophoroid group, Table 4 lists genera included in each group). Justifications for branchings are given below.

The Fideliidae (Fig. 30) are distinguished by elongated outer and inner cardinal processes, that form a u-shaped articulation with the basistipital process (Fig. 3a) (19); and by the subligular process that is separated from the prementum by a membranous or lightly sclerotized area (Fig. 12a) (20). Other characteristics of the group include thickened sclerotization along the premental fold (apical to the base of the ligular area), absence of a stipital comb, plumose stipital hairs, short and narrow basistipital process, apically widened stipital sclerite, and a slightly concave apex of the mentum.

The genera of the Nomadinae (Fig. 31) (except *Thalestria* and *Triepeolus*) are united by the elongate inner cardinal process (Fig. 3c) (17), similar to that of the Fidellidae, but lack an elongated outer process. Also, the basal process of the prementum is convexly curved (Fig. 10c) (18). Within the Nomadinae, two principal subgroups are apparent, *Leiopodus, Caenoprosopis, Nomada,* and *Holcopasites,* with no stipital comb (11) and *Biastes* which has a weak stipital comb. The nomadines also have few or no hairs on the stipes and lacinia, four- to six-segmented maxillary palpus, and a reduced stipital sclerite.

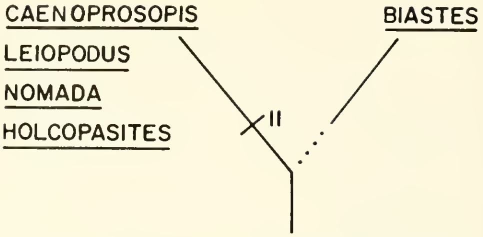

Fig. 19: Dendrogram showing relationships among proboscides of Nomadinae group. There are no synapomorphic characters shown for *Biastes*.

Another distinctive group is formed by anthophorid bees having an elongated paraglossae (23), the eucerines, melectines, and *Canephorula* (Fig. 20). The eucerines (Fig. 32) and *Canephorula* differ from the melectines by the length of the paraglossa (which extends to the apex of the glossa (Fig. 16c) (25), the presence of a stipital comb, and striations in the membrane underlying the lacinia (26).

The Eucerini (Fig. 32) form a homogenous group. The area between the subgalea and stipital sclerite is partly sclerotized (27), and the base of the stipes is expanded along the anterior margin (Fig. 4a). Eucerines have long, plumose hairs along the basal posterior margin of the stipes, a stipital comb, and an elongated cardo. *Canephorula* resembles the eucerines in many characters, but differs in the prementum, which is partly membranous and flattened (Fig. 12g) (28), unique among all the bees. Also, *Canephorula* has no sclerotization in the subgalea-stipital sclerite region. For these reasons, it has been placed in a separate group, but with affinity to the eucerines.

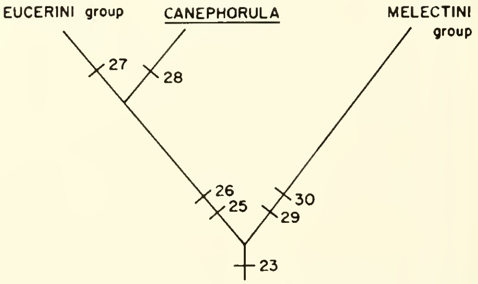

Fig. 20: Dendrogram showing relationships among proboscides of Eucerini and Melectini groups.

The melectines (Fig. 33) are characterized by paraglossae extending two-thirds of the length of the glossa (23), a brush on a small expanded lobe of the palpiger (Fig. 33) (29), a stipital sclerite which terminates basal to the basigaleal area (Fig. 9c), a convex basal premental process (Fig. 10c), and lack of a stipital comb (11). Also, there are three bristles on a membranous fold basal to the basigaleal area; the melectines are the only long-tongued bees with such setae (Fig. 9c) (30). Other characteristics of the melectines include the shape of the stipes (similar to Fig. 4g), elongated lacinia (Fig. 8f), bifurcated mentum (Fig. 10c), and broad attachment of the paraglossa to the paraglossal suspensorium (Fig. 16d). Phenetically, the melectines do not show close affinity with the Eucerini-*Canephorula;* presumably elongated paraglossa evolved separately in the two groups.

A large group is formed by the Apidae, Xylocopinae, and the Exomalopsini, Tetrapediini, Centridini, and Anthophorini of the Anthophorinae (Figs. 21, 22). While no apomorphous proboscidial characters unite all these bees, the recurrence of many characters in varied genera of this group suggests relationship among its members. These characters include the broad attachment of the paraglossa to the paraglossal suspensorium (Fig. 16a) (all except Tetrapediini and *Anthophorini* groups); the five- to six-segmented maxillary palpi (*Xylocopa, Centris, Anthophora, Caenonomada, Ceratina, Manuelia, Allodape, Braunsapis, Exomalopsini*); the presence of a stipital comb (all but the allodapines), a bipartite stipital thickening (Fig. 5c) (Xylocopini, *Manuelia,* allodapines, *Apis*); the broad, membranous or lightly sclerotized, and hairless or slightly hairy lacinia (Fig. 8e) (*Apis, Ceratina, Manuelia,* allodapines); and the long, abundant, and often plumose stipital hairs (*Centris, Anthophora, Amegilla,* Exomalopsini, Xylocopini).

The Anthophorinae most similar to the Xylocopinae-Apidae group can be differentiated into two branches, the Anthophorini group and the Exomalopsini-Tetrapediini groups (Fig. 21). The Anthophorini group (Fig. 34) differs from the latter in the unique extended apical end of the subligular process, forming a u-shaped structure upon which the glossa rests (Fig. 12f) (24). Other characteristics of the Anthophorini group include the straight and apically broadened stipital sclerite, curving anteriorly basally (Fig. 6g), the hairless or sparsely hairy lacinia, the slightly concave apex of the mentum (Fig. 10a), and the comb and plumose posterior hairs of the stipes (Fig. 4d).

Tetrapedia differs from the Exomalopsini group by the expanded apical end of the stipital sclerite (Fig. 6e), lack of a broad attachment of the paraglossa to its suspensorium (Fig. 16b), and the shape of the subligular process, narrowed apically and basally and expanded medially (Fig. 12c) (31). Exomalopsini (Fig. 35) have a broadly attached paraglossa (Fig. 16a), non-expanded stipital sclerite, a triangular subligular process (Fig. 12e), and a brush on the first segment of the labial palpus similar to that of lithurgines (Fig. 11a) (13), although not as well-developed. Also, the exomalopsines have a sclerotized ridge medially along the outer surface of the apical third of the stipes (Fig. 4j) (32); this ridge is lacking in *Tetrapedia. Caenonomada* has a unique hooked inner cardinal process (Fig. 3d).

The Xylocopinae-Apidae group (Fig. 22) is divided into three branches by differentiation of the stipital sclerite. In Xylocopini and Meliponinae, each end of the stipital sclerite is expanded into a triangular process, the larger apical process usually extending as far as the inner margin of the subgalea (Fig. 6i) (35). In the allodapines and the *Ceratina* group, the stipital sclerite is slender and slightly curved, and expanded into a small apical knob (Fig. 6d) (33). The stipital sclerite of Apidae, except Melipo-

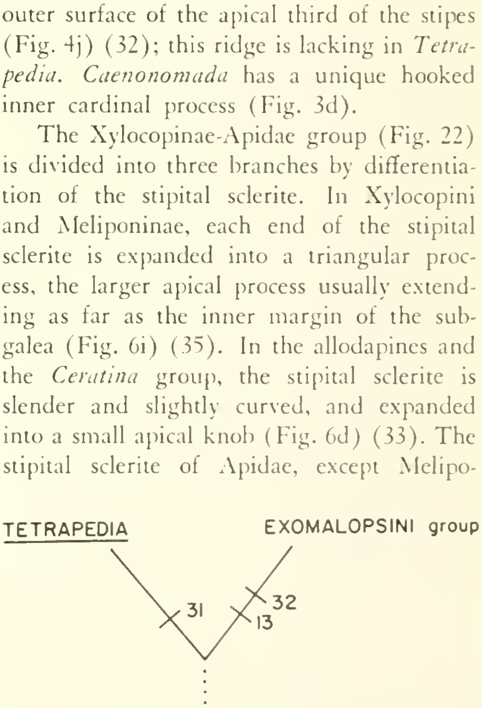

FIG. 21: Dendrogram showing relationships among proboscides of Exomalopsinae.

ninae, varies but is never like that of the other groups (Figs. 6b, c, h). The paraglossa is broadly attached to the paraglossal suspensorium in the entire group (Fig. 16a).

Ceratina (Fig. 36) and *Manuelia* differ from the allodapine bees (Fig. 37) in having a stipital comb; the allodapines are combless (11). Both groups have sparse posterior stipital hairs, a relatively short and broad basistipital process, and a broad, lightly sclerotized, hairy lacinia.

The Xylocopini-Meliponinae group is distinguished by its stipital sclerite (35), as described above, by the strongly bifurcate mentum (Fig. 10c), and by the robust anterior longitudinal brace (34). The Xylocopini (Fig. 38) form a particularly distinctive group, with heavily sclerotized maxilla, almost square stipes with a strongly curved comb indentation and extremely robust comb teeth (Fig. 4h) (36), short cardo, and bipartite stipital thickening (Fig. 5c) (37) with an expanded sclerotized area where the two parts meet. Also, the stipital sclerite is fused with the apical end of the stipital thickening, and in some species of *Xylocopa* (*X. varipuncta* and *fimbriata*) it is also fused with the stipes. Meliponinae (Fig. 39) are characterized by long, posterior bristles on the stipes (Fig. 4i), one-segmented maxillary palpus, and a long basistipital process, extending to the submentum, formed largely by the basistipital thickening (Fig. 5b) (38). *Melipona* has hairs along the posterior edge of the stipes (Fig. 39).

Apinae (*Apis*, Fig. 40) differs from Bombinae (Euglossini and Bombini) by the weak stipital comb (39), the membranous, hairless lacinia (Fig. 8e) (41), and the unique bulla on the inner cardinal process (Fig. 3f) (40). (To my knowledge, this is the first report of a stipital comb in *Apis;* this structure appears to have been overlooked by previous authors.) Bombini (Fig. 41) have a unique, strongly sclerotized ridge where the cardo diverges into the cardinal processes (Fig. 3e) (42) (not visible in Fig. 41 due to the orientation of the specimen). The stipital sclerite of the bombines is similar to that of the Meliponinae in being somewhat expanded apically, suggesting that this trait may be primitive for Apidae. Euglossini (Fig. 42) is distinguished by the extremely long glossa, labial palpus, and galea (43).

The remaining Anthophorinae form three groups, *Melitoma-Diadasia, Mesocheira-Ericrosis,* and *Thalestria-Triepeolus. Melitoma* and *Diadasia* (Fig. 43) are characterized by slight enlargement of the apical end of the stipital sclerite both anteriorly and posteriorly (Fig. 6f); a brush on the third segment of the maxillary palpus (Fig. 11b) (21); broad, membranous, and hairless lacinia (Fig. 8e); sparse plumose hairs along the entire precomb region of the stipes; and a weak stipital comb. *Melitoma* differs from *Diadasia* in having elongated glossa, labial palpus, and galea, as well as in the shape of

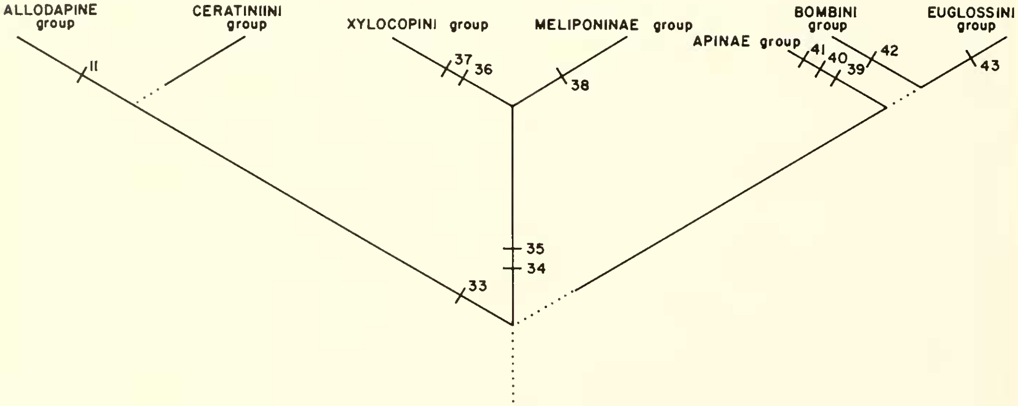

Fig. 22: Dendrogram showing relationships among proboscides of Xylocopinae and Apidae groups. Dotted lines indicate groups for which there are no synapomorphic characters.

the mentum (slightly concave apically in *Melitoma*, bifurcate in *Diadasia*).

Mesocheira (Fig. 44) and *Ericrocis* are similar in their broad lacinia, enlarged basal process of the prementum, bifurcate mentum (Fig. 10c), stipital shape (Fig. 4e), weak stipital comb, and rectangular subligular process (like Fig. 12d). For *Thalestria* and *Triepeolus* (Fig. 45), common characters include stipital shape (similar to Fig. 4g), expanded sclerotization of the junction of the stipital and basistipital thickenings (Fig. 5e) (22), broad and hairless lacinia, loss of the stipital comb (11), and a bifurcate mentum (Fig. 10c).

DISCUSSION

In the preceding sections, the comparative morphology of the proboscides of the long-tongued bees is described and a cladistic analysis of mouthpart characteristics is presented. These provide some insights into the taxonomy and phylogeny of the long-tongued bees. Instances where the present results support or disagree with current classification and phylogeny of the bees (Table 1, Michener, 1944, 1974a) will be discussed below. However, I shall not reclassify the bees; such a reclassification should be based on more characters than those of the labiomaxillary complex alone.

This study supports a monophyletic origin (Ashlock, 1971) for all long-tongued bees, the families Anthophoridae, Apidae, Fideliidae, and Megachilidae. Species in a monophyletic group must share synapomorphous characters, or unique evolutionary innovations. For long-tongued bees, such characters include the long glossa, the long and flattened first two segments of the labial palpus, the long galea, the terminal flabellum on the glossa, the internal sclerotized glossal rod (not examined for all specimens, but present in all those examined), the anterior curvature of the subligular process, the galeal midrib, the shape and articulations of the mentum and submentum, the well-developed paraglossal suspensorium, and the presence in many genera of a stipital comb. The complexity of these characters and their functional interdependence, as well as their universality among long-tongued bees, strongly suggest monophyly. Further, since there is no evidence that other groups evolved from members of this mouthpart group, it can be considered holophyletic (Ashlock, 1971).

Michener (1944, 1974a) considered Melittidae among short-tongued bees to be the closest to long-tongued bees because of the morphology of the postmentum. Melittid characters (for *Melitta* and *Ctenoplectra*) such as the form of the mentum and lorum, ligular arm similar to that of Lithurginae (Fig. 14b), and a somewhat elongated basistipital process (L. Greenberg, in prep.) are similar to those of long-tongued bees. The distinct ligular arm of *Melitta* and *Ctenoplectra* may be derived from the fused condition found in other *Melittidae*, many short-tongued bees, and the sphecoid wasps (R. McGinley, pers. comm.); fusion of the ligular arm to the prementum in the antnophorid group is thus likely to be secondarily derived. Alternatively, the anthophorid group might be primitive in this character, with *Melitta, Ctenoplectra,* and Megachilidae united by their free ligular arms. This interpretation appears unlikely, however, as it would require that the elongated glossa be evolved separately in the Megachilidae and the anthophorid gorup. The ligular arm should be re-evaluated in a study of short-tongued bees to determine the homologies of various types of fusions and separations. The short-tongued bee *Ctenoplectra*, considered to be a melittid (Michener, 1944, 1974a), is similar to long-tongued bees for most characters, excluding the length of the glossa, galea, and labial palpus. *Ctenoplectra* and long-tongued bees can be considered sister groups.

The classification of Megachilidae according to mouthpart characters generally agrees with that of Michener (1944, 1974a). Megachilidae diverge from other long-tongued bees in having a dististipital process (except for *Dioxys*) and ligular arms which do not merge with the premental fold basally, but rather rest freely in the membrane of the premental concavity (the proposed primitive condition for long-tongued bees). Thus, their distinctiveness as a family seems justified by mouthpart characteristics. Within the Megachilidae, the Lithurginae and the Megachilinae are distinct from one another, the Megachilinae with short ligular arms and the Lithurginae with long ones and a brush on the first segment of the labial palpus, absent in Megachilinae. The tribes Megachilini and Anthidiini of Megachilinae are scarcely distinguishable; they would not have been separated on the basis of the proboscis alone.

Dioxys, previously classified either as an anthidiine (Michener, 1944) or as a separate subfamily (Popov, 1947), differs from anthidiines in important labiomaxillary characters, such as reduced lacinia and lack of a dististipital process. Non-mouthpart characters (reduced sting, absence of a scopa) support placement of *Dioxys* in a separate group, possibly as a tribe of Megachilinae. *Coelioxys* (in Megachilini according to Michener, 1944) has an anthidiine-like lacinia and lacinial comb, as well as a scutellum separated into dorsal and posterior surfaces by a distinct angle, an anthidiine characteristic (Michener, 1944); re-examination of its taxonomic position may also be warranted. *Anthidium*, *Immanthidium*, and *Callanthidium* are unique among Megachilidae in having stipital combs, probably a convergent feature rather than a synapomorphous character uniting these genera with other groups possessing stipital combs. Independent origin of the stipital comb in this group is suggested by the lack of such a comb among all other megachilids, the irregular occurrence of the comb in members of the anthophorid mouthpart group, and the similarity of *Anthidium*, etc., to the other Anthidiini in other mouthpart characters.

Of some interest is the placing of Fideliidae with the anthophoroid group rather than Megachilidae, where it is placed by Rozen (1970, 1977) (Figs. 18a, b). While fideliid larvae show similarities to those of megachilids, the fusion of the ligular arm with the premental fold (a synapomorphous character for the anthophoroid line) as well as non-mouthpart characters (mandibular structure, independent volsellae, and wing venation, Michener, 1944) support recognition of the Fideliidae as a separate family. However, the extended region of sclerotization along the premental fold apical to the point where the ligular arm merges with it in Fideliidae (Fig. 30) may be homologous with the extended base of the ligular arm characteristic of Lithurginae (Fig. 14b). If so, Fideliidae might be grouped with the Lithurginae, but this grouping would require independent origin of the fused ligular arm in Fideliidae and the anthophoroid group.

A close relationship between the Meliponinae and the Xylocopinae is indicated by mouthparts (Winston and Michener, 1977). While non-mouthpart characters (such as presence of a corbicula) support the inclusion of the Meliponinae in the Apidae, the mouthpart similarities of this subfamily to the Xylocopini suggest early divergence of the Meliponinae from the other apids.

Some affinities appear, on the basis of similarities recurring in some but not all genera, between the Xylocopinae and certain tribes of Anthophorinae (Exomalopsini, Tetrapediini, Centridini, and Anthophorini). More and better (i.e., synapomorphous) characters would be needed to justify recognition of such a group; however, it may be that these tribes of Anthophorinae share a common ancestor with the Xylocopinae. Within the Xylocopinae, the allodapine bees stand out as a group distinct from the Ceratini and Xylocopini. The allodapines have not been considered as a taxon (Michener, 1974a); if other characters support their distinctiveness, they should be considered as a separate tribe (Allodapini) of the Xylocopinae.

On the basis of similarities in mandibular structure, Michener and Fraser (1978) have suggested that the Xylocopinae and Lithurginae (Megachilidae) may be related. The structures of the labiomaxillary complexes do not support this idea; both are among the most distinctive of the mouthpart groups. Mandibular similarities between Xylocopinae and Lithurginae thus appear to reflect convergent evolution, presumably related to their wood-nesting habits.

Triepeolus and *Thalestria*, both Nomadinae according to Michener (1944) and others, are not included in the Nomadinae mouthpart group. Their distinctive mouthparts suggest that these genera may not be closely related to other Nomadinae.

The position of *Canephorula* as a sister-group to the Eucerini was suggested by Michener (1944). Although in that classification it was included in Eucerini, *Canephorula* was separated into a tribe of its own by Michener et al. (1955). The present study supports placing *Canephorula* in a sister tribe (*Canephorulini*) to Eucerini on the basis of synapomorphous characters of the two groups. The placement of *Thyreus* and *Meleeta,* on the basis of mouthparts, as a sister group of the Eucerini and Canephorulini is not supported by other characters (Michener, 1944). Although these groups have what could be considered as a synapomorphous character, the elongated paraglossa, they are otherwise extremely distinct. The elongated paraglossa appears to be convergent rather than synapomorphous.

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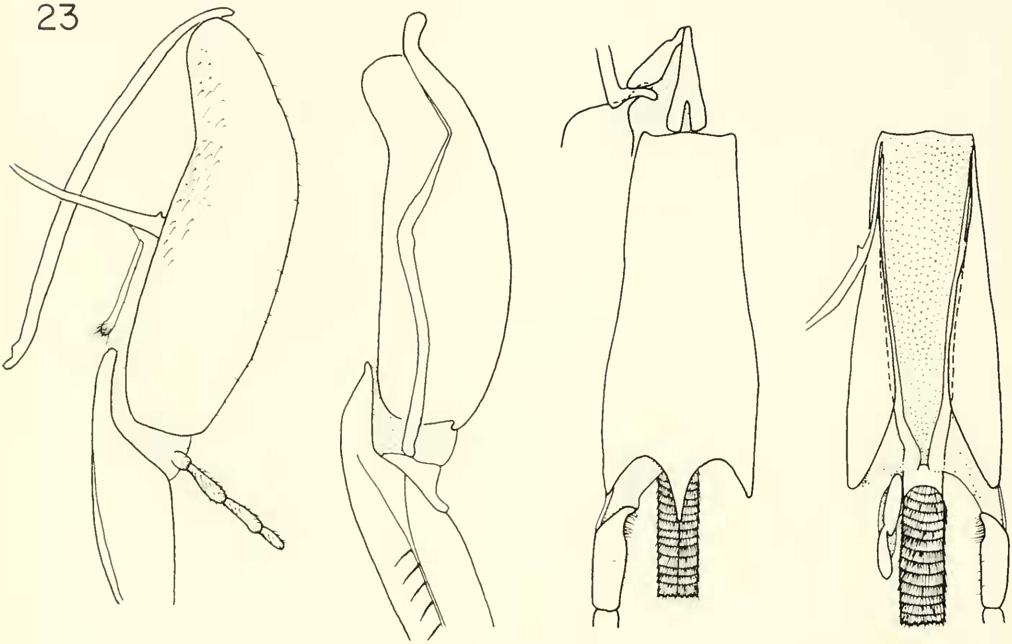

FIG. 23: *Lithurge gibbosus.*

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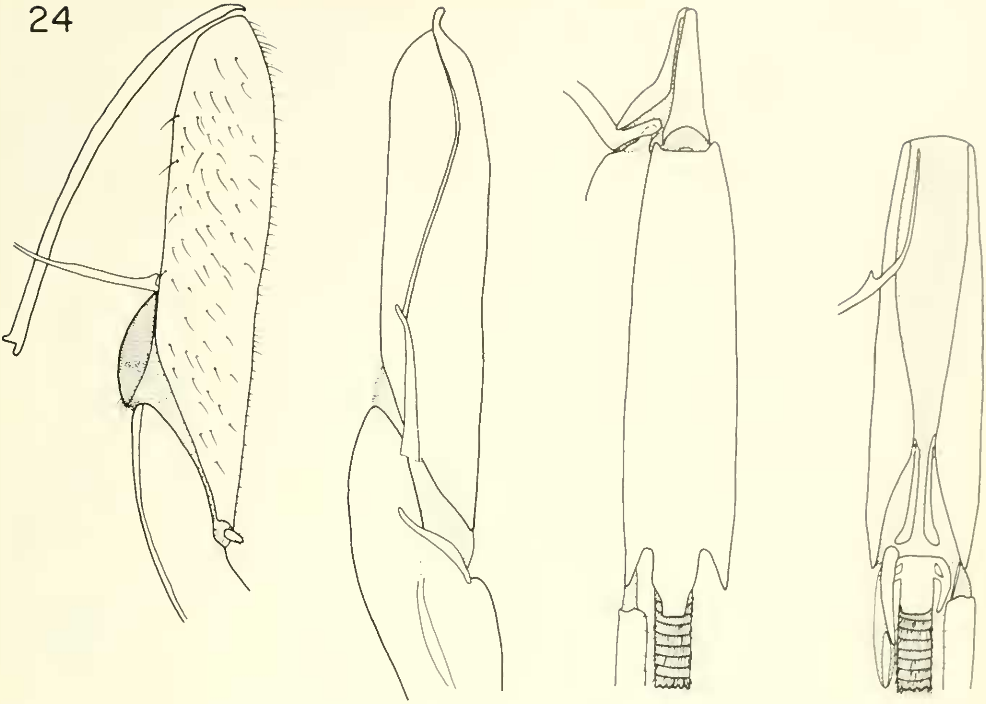

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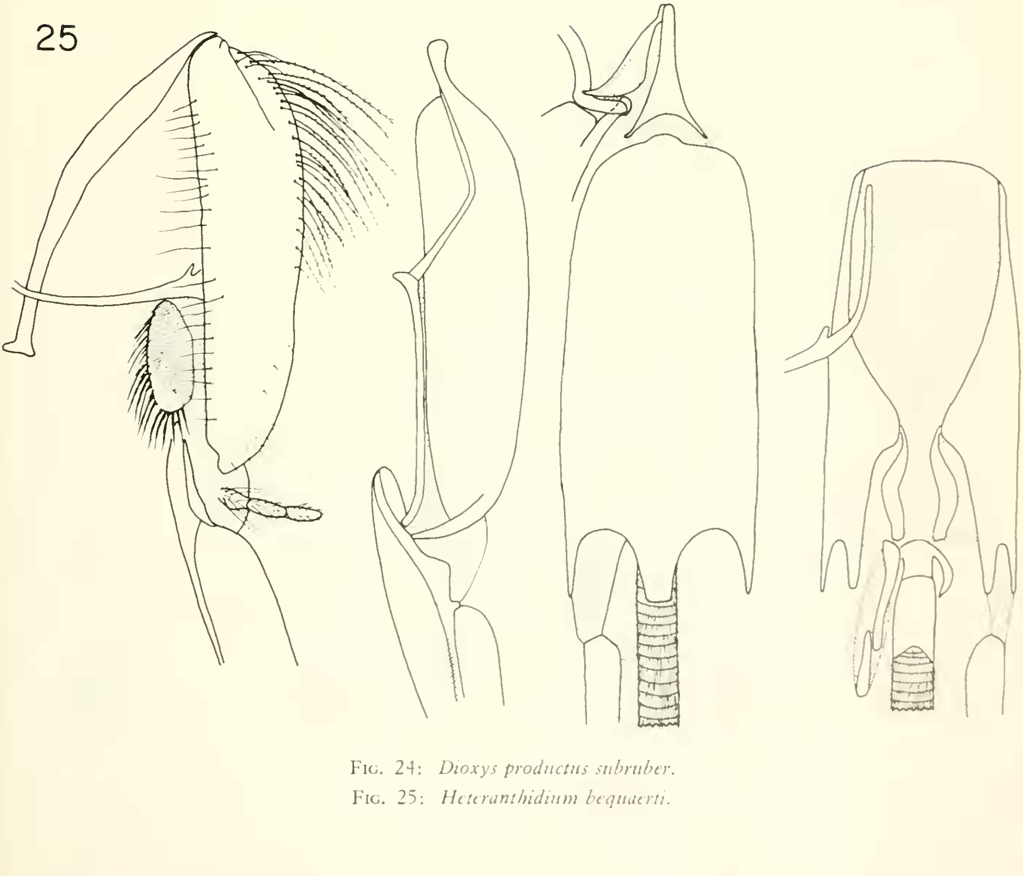
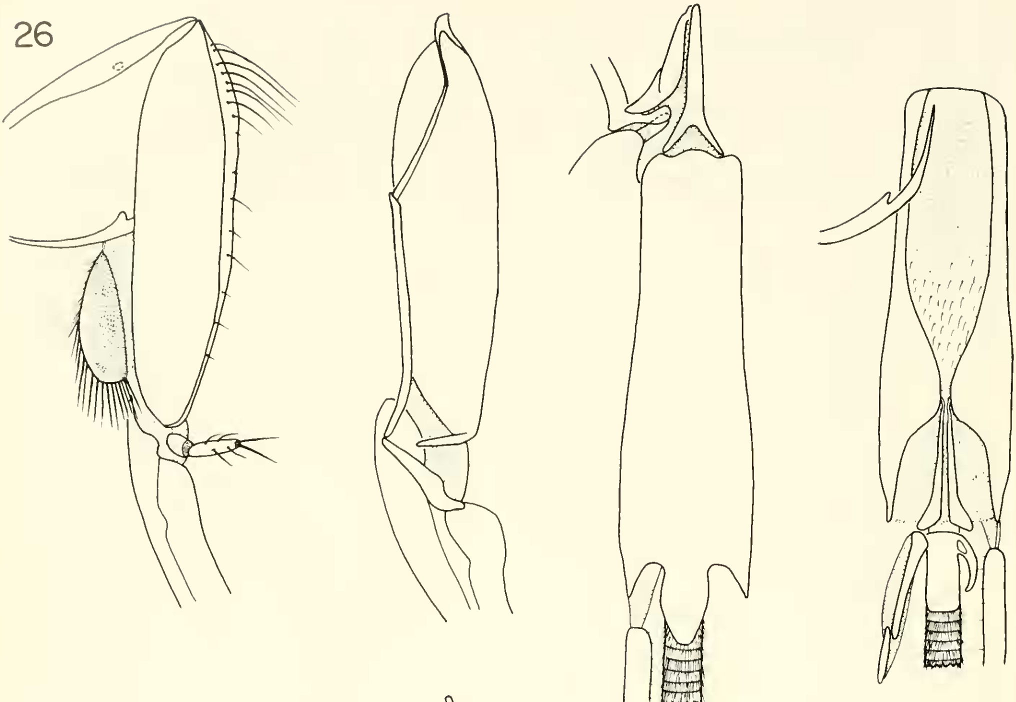


Fig. 24: *Dioxys productus subruber.*

Fig. 25: *Heteranthidium bequaerti.*

26



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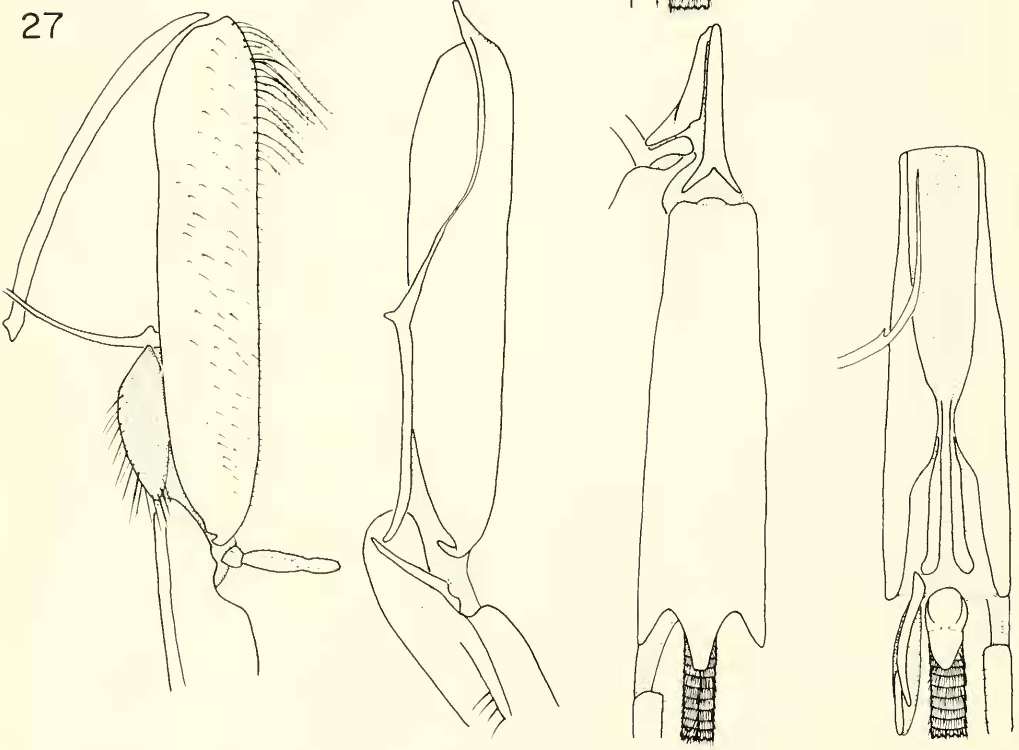
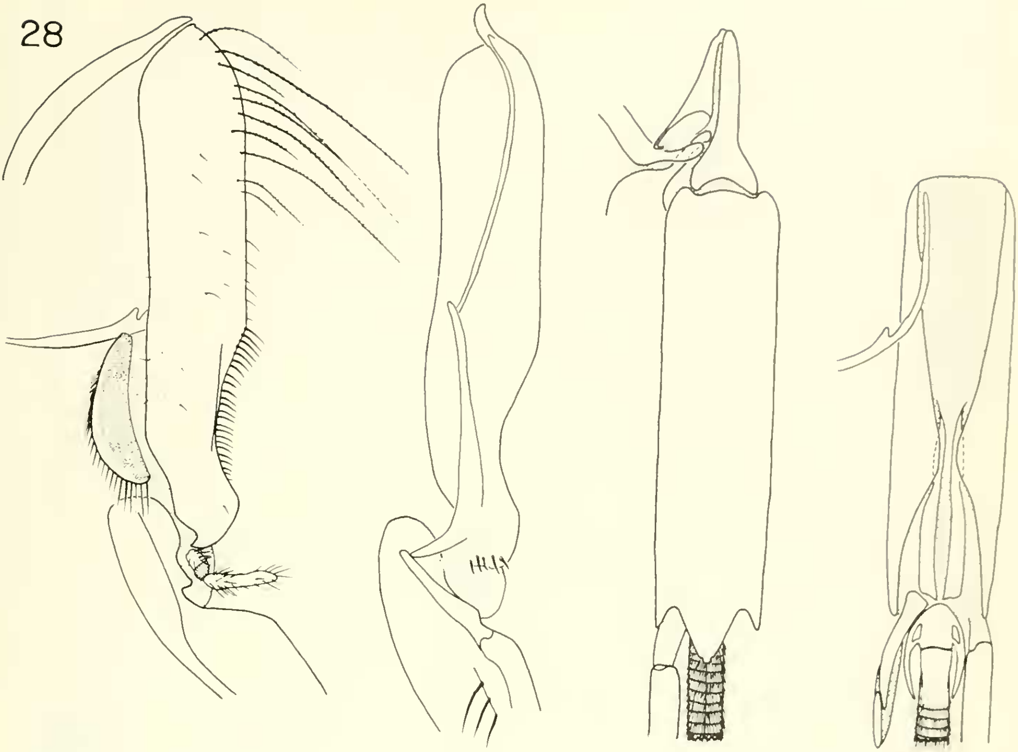


Fig. 26: *Hypanthidium taboganum.*
Fig. 27: *Stelis atterima.*

28



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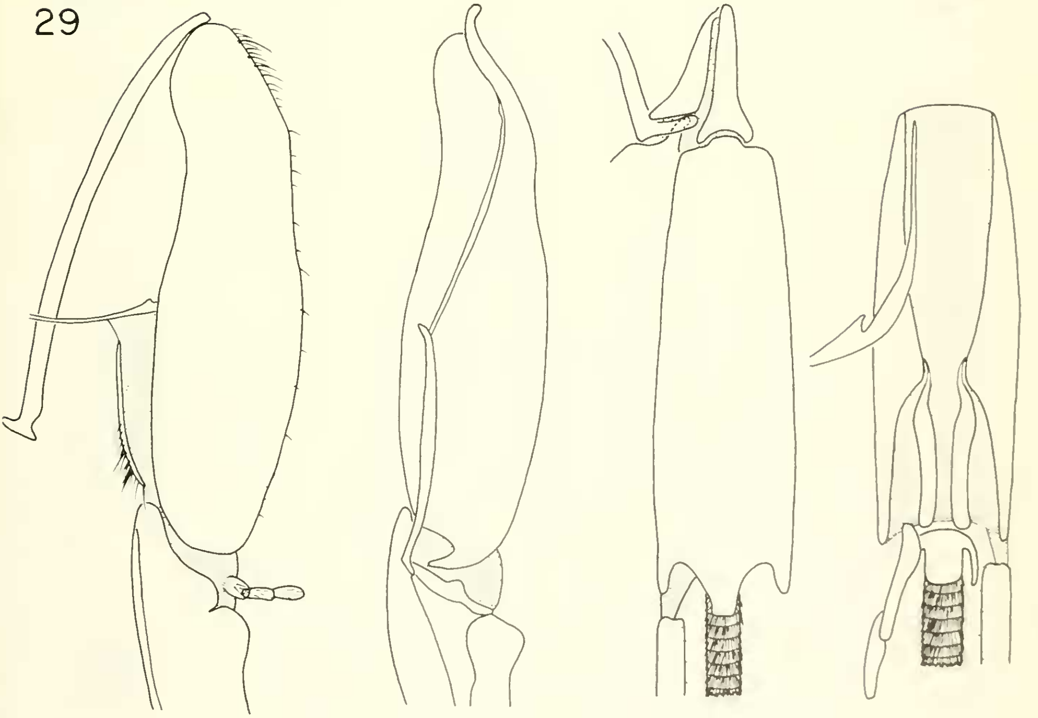
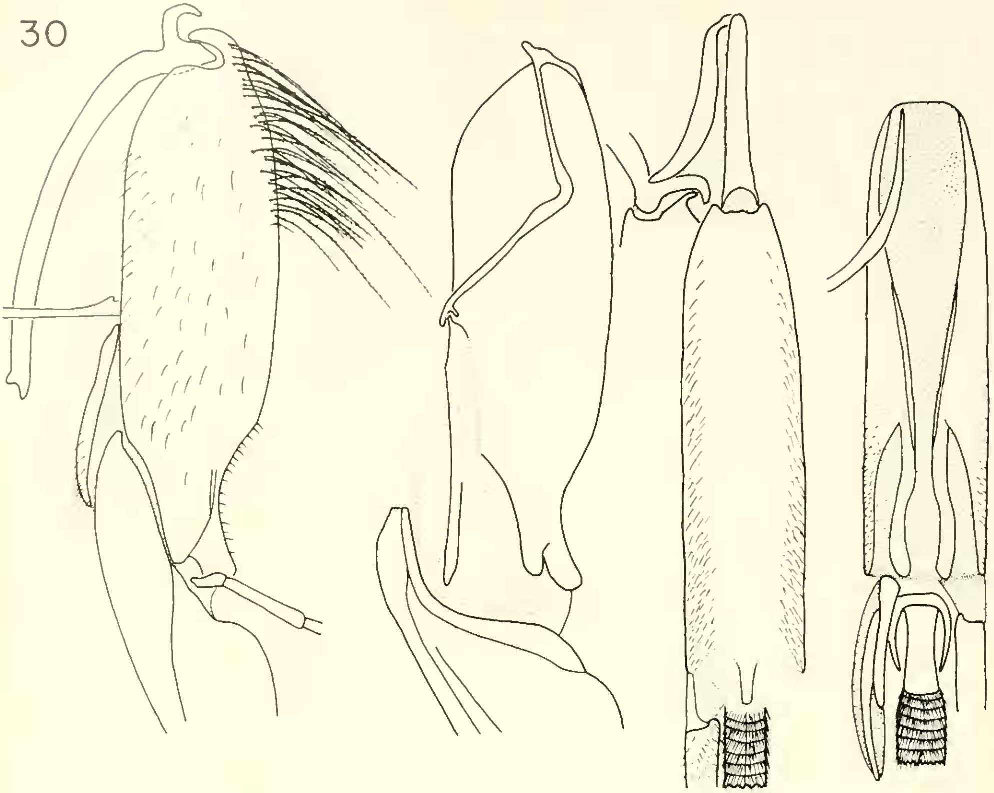


Fig. 28: *Anthidium manicatum.*

Fig. 29: *Megachile albitarsis.*

30



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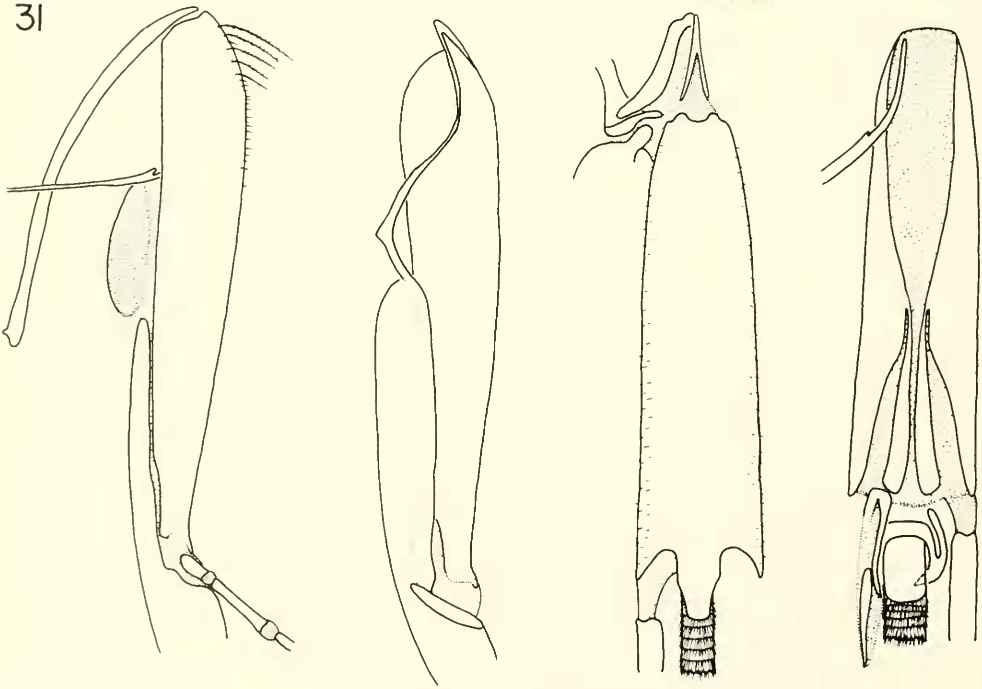

Fig. 30: *Neofidelia profuga.*

Fig. 31: *Nomada annulata.*

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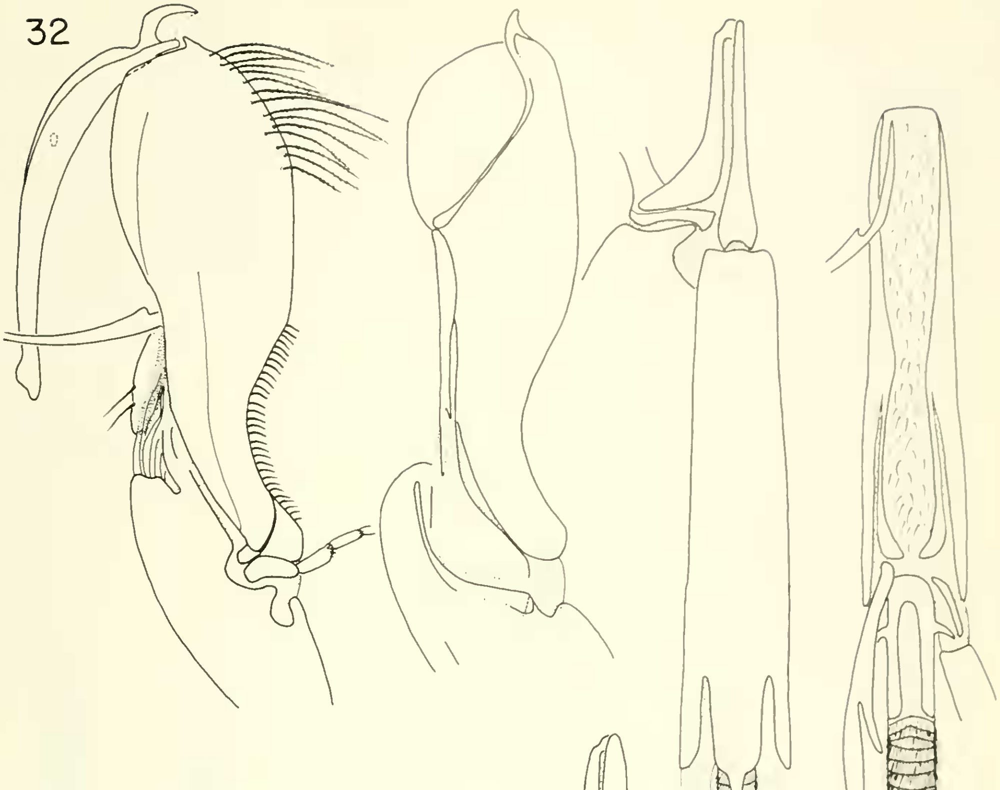

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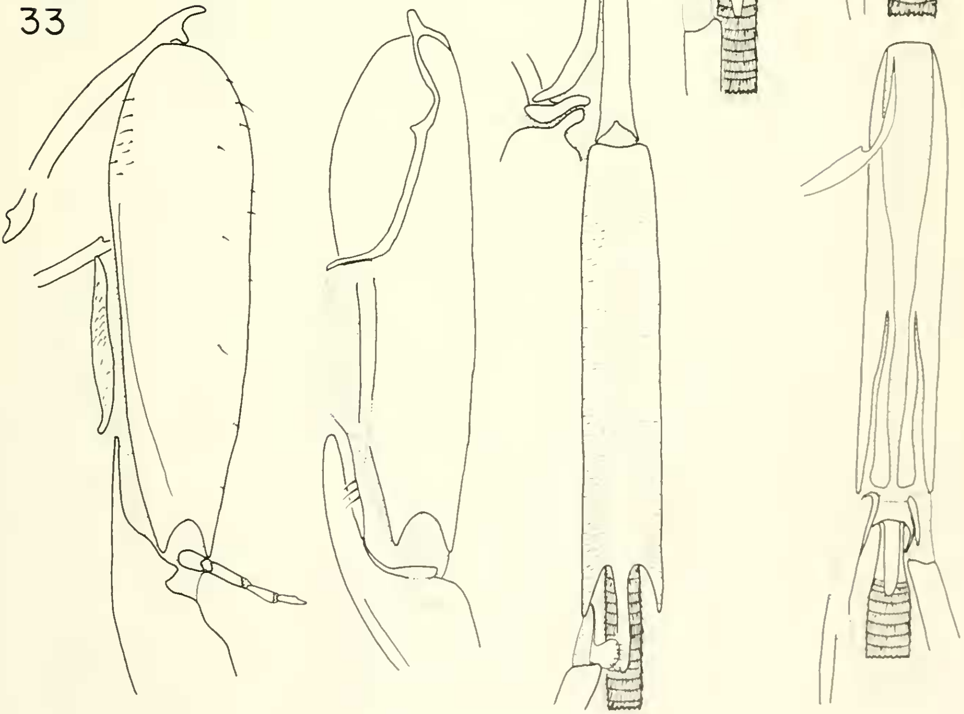

FIG. 32: *Eucera chrysopyga.*
FIG. 33: *Melecta californica.*

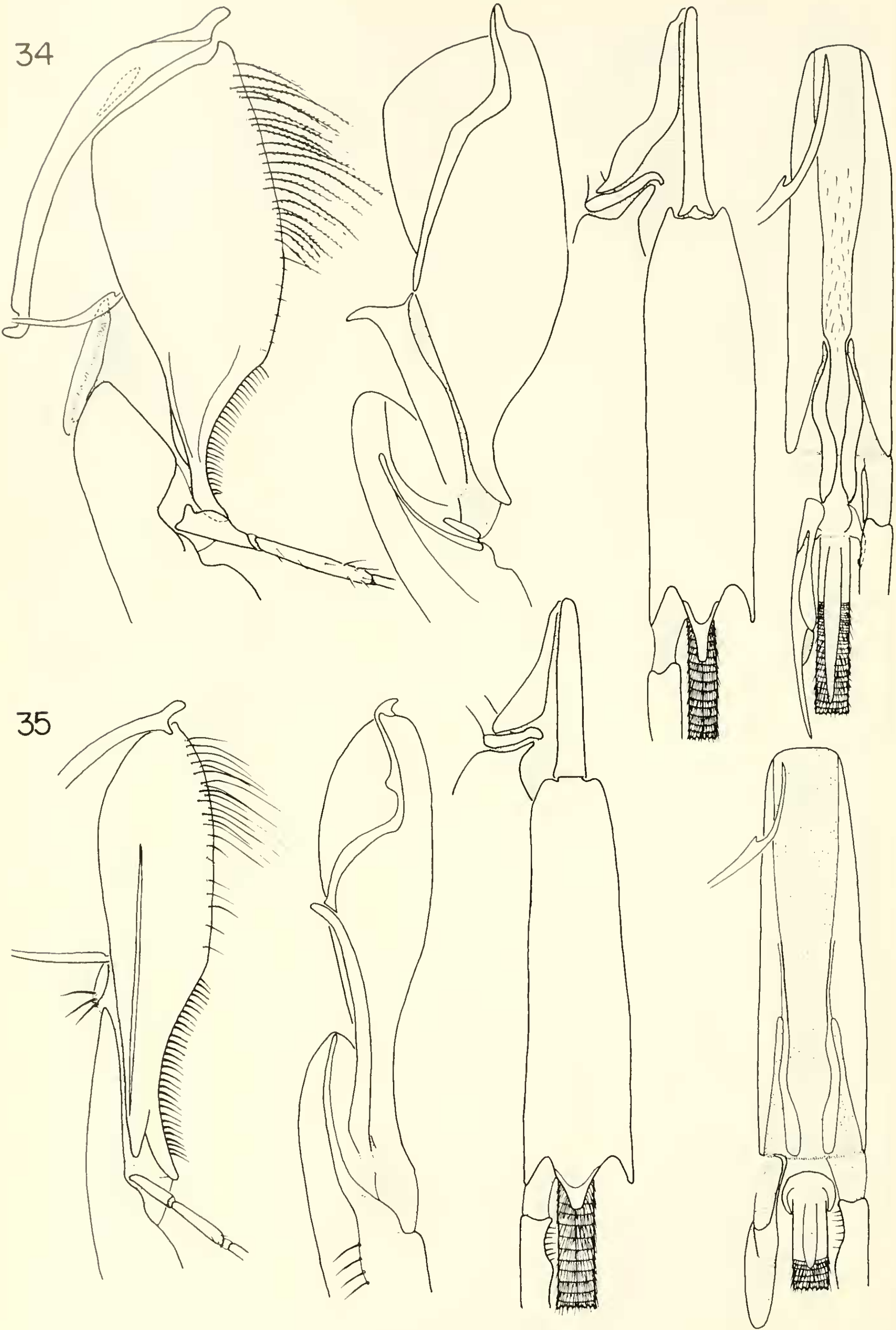

FIG. 34: *Anthophora occidentalis.*
FIG. 35: *Exomalopsis zexmeniae.*

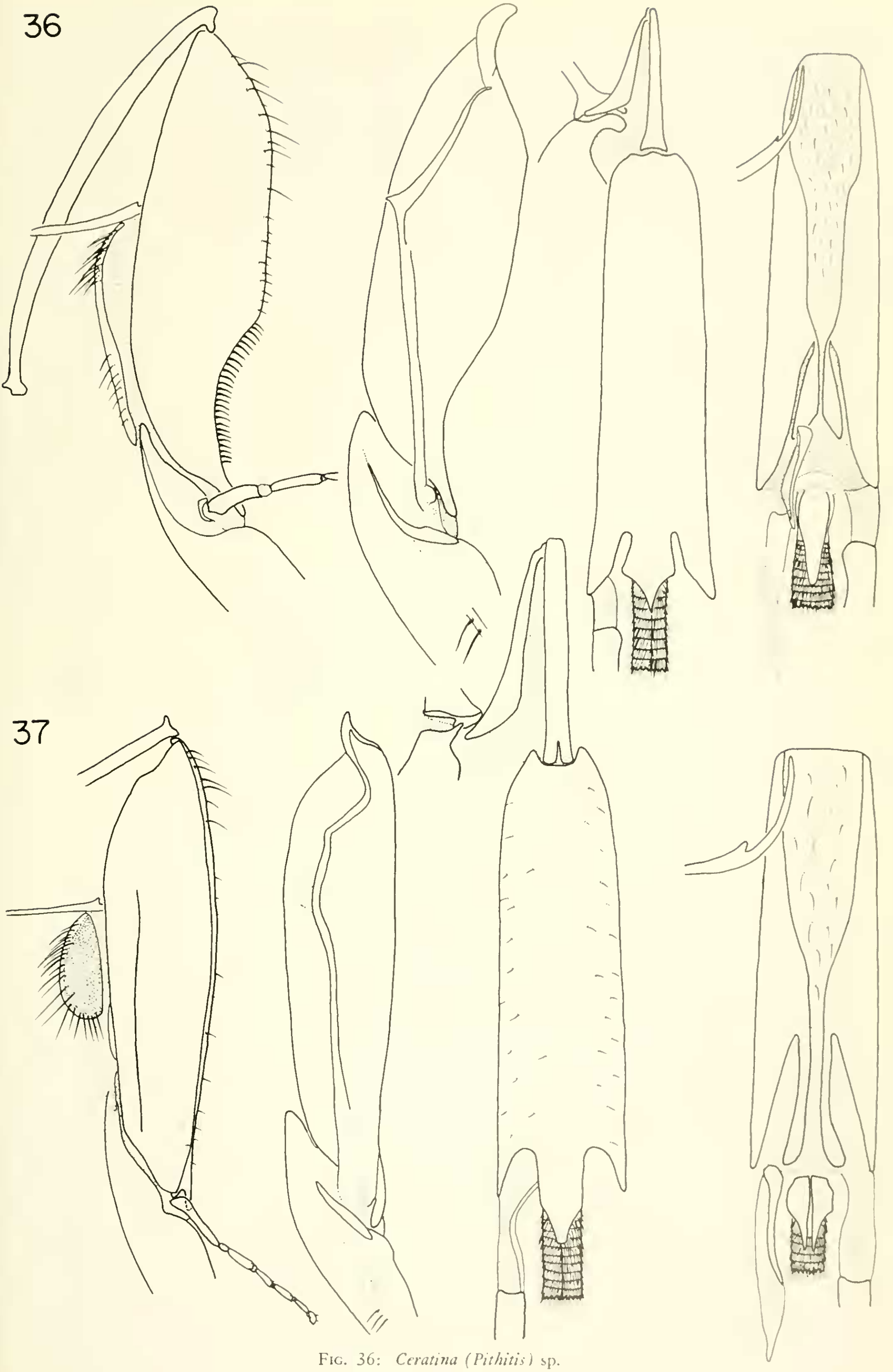

Fig. 36: *Ceratina (Pithitis)* sp.
Fig. 37: *Allodape stellarum.*

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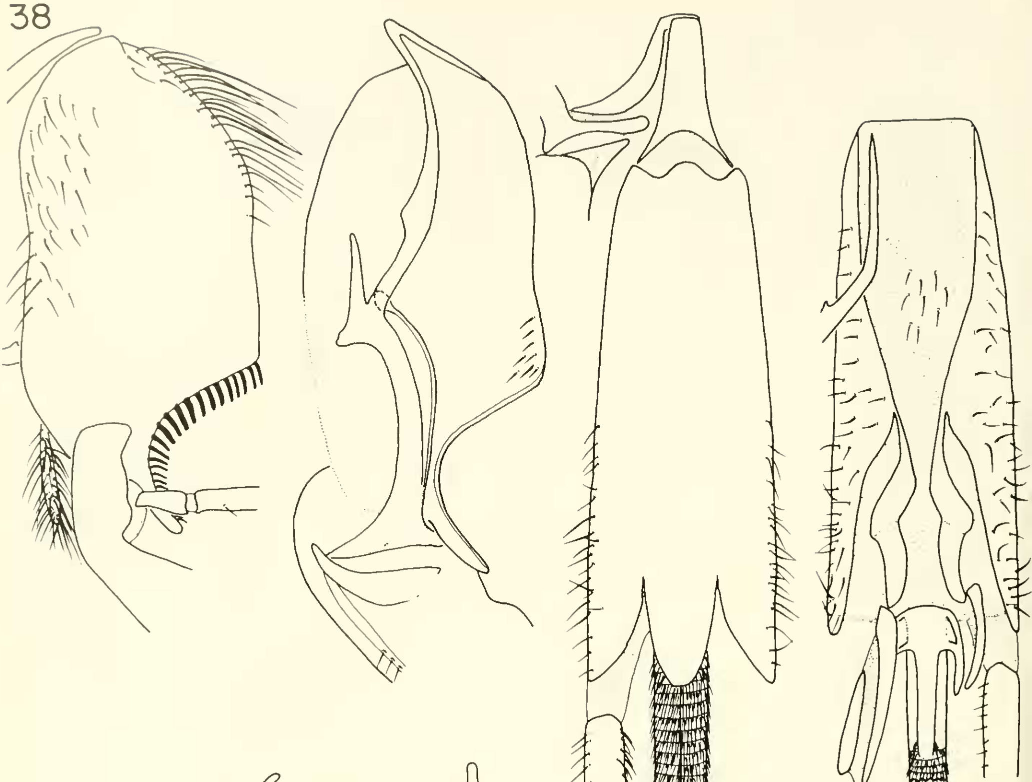

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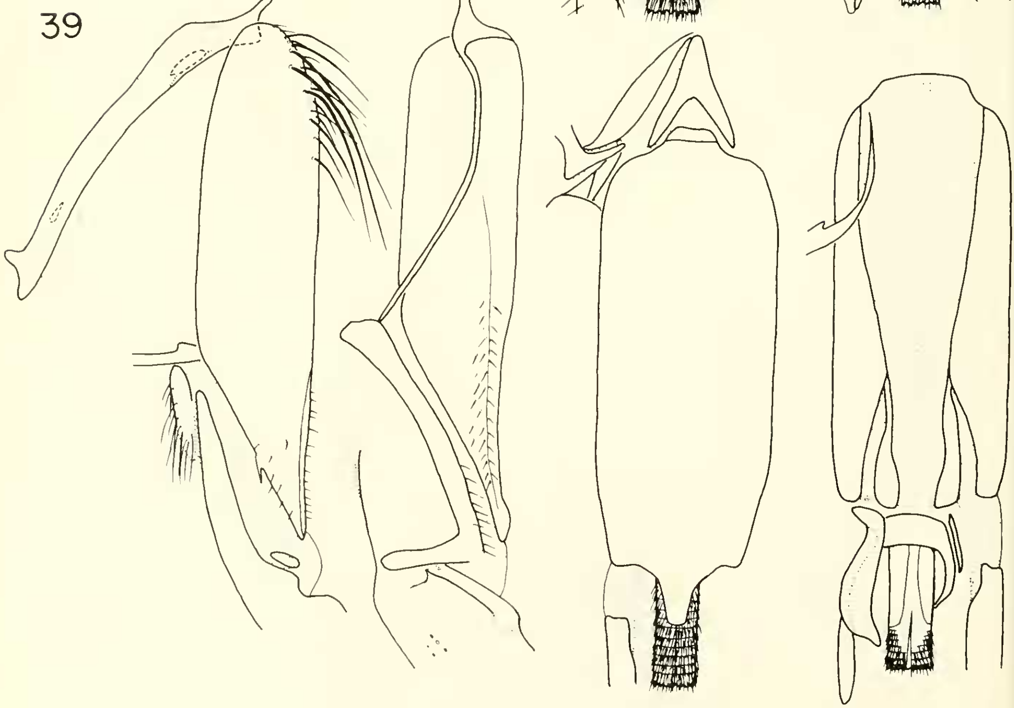
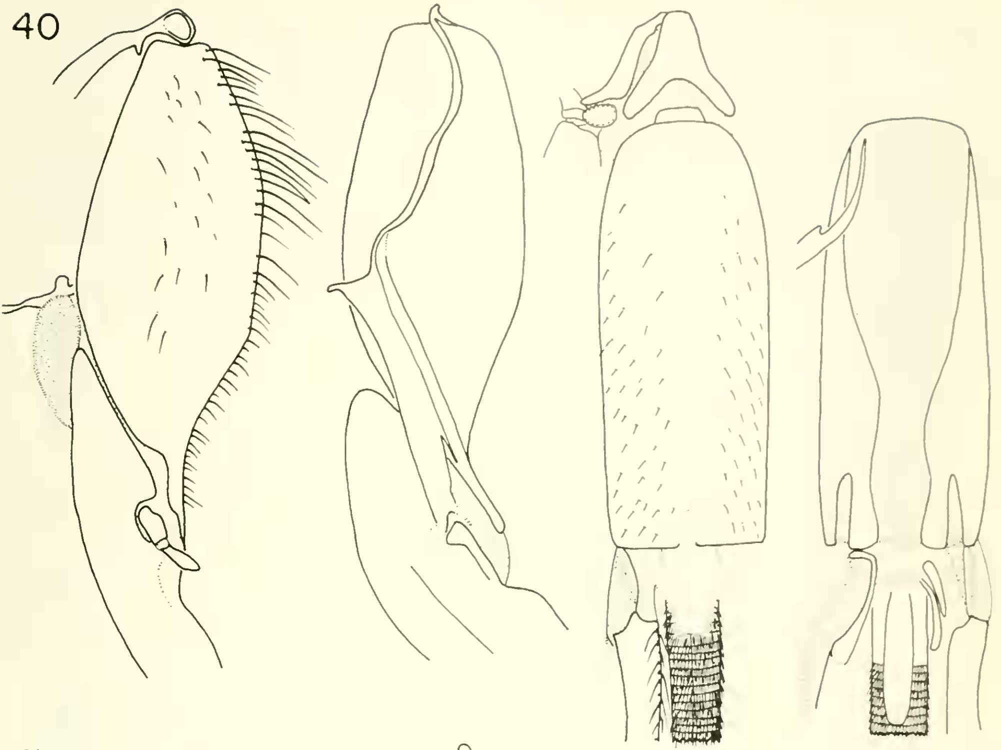


Fig. 38: *Xylocopa virginica.*

Fig. 39: *Melipona fasciata.*

40



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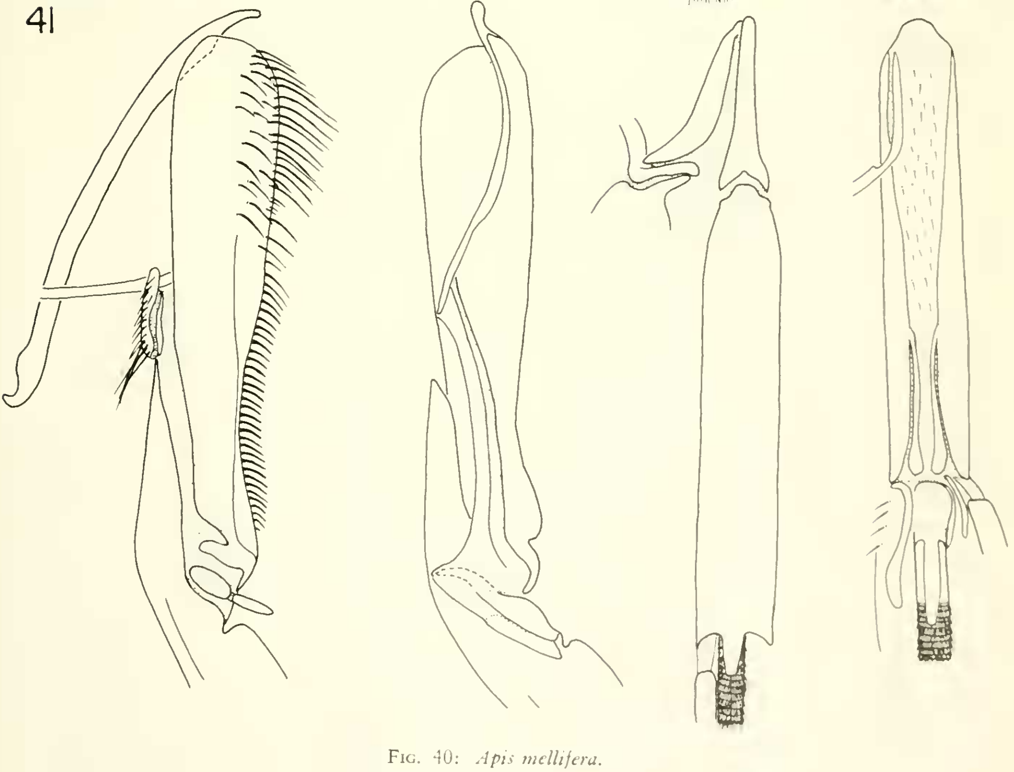

Fig. 40: *Apis mellifera*.

Fig. 41: *Bombus americanorum*.

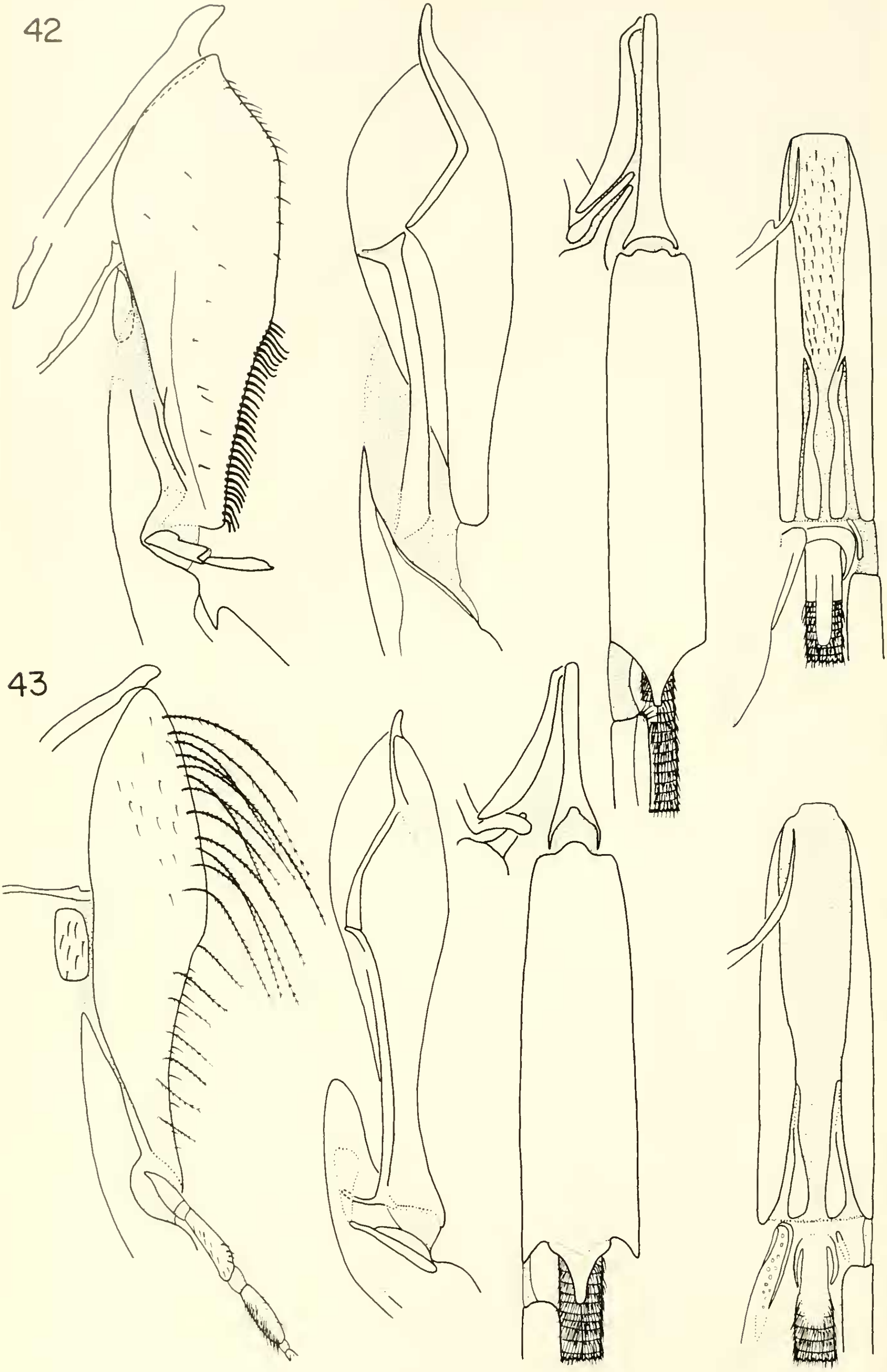

FIG. 42: *Euplusia violacea.*
FIG. 43: *Diadasia afflicta.*

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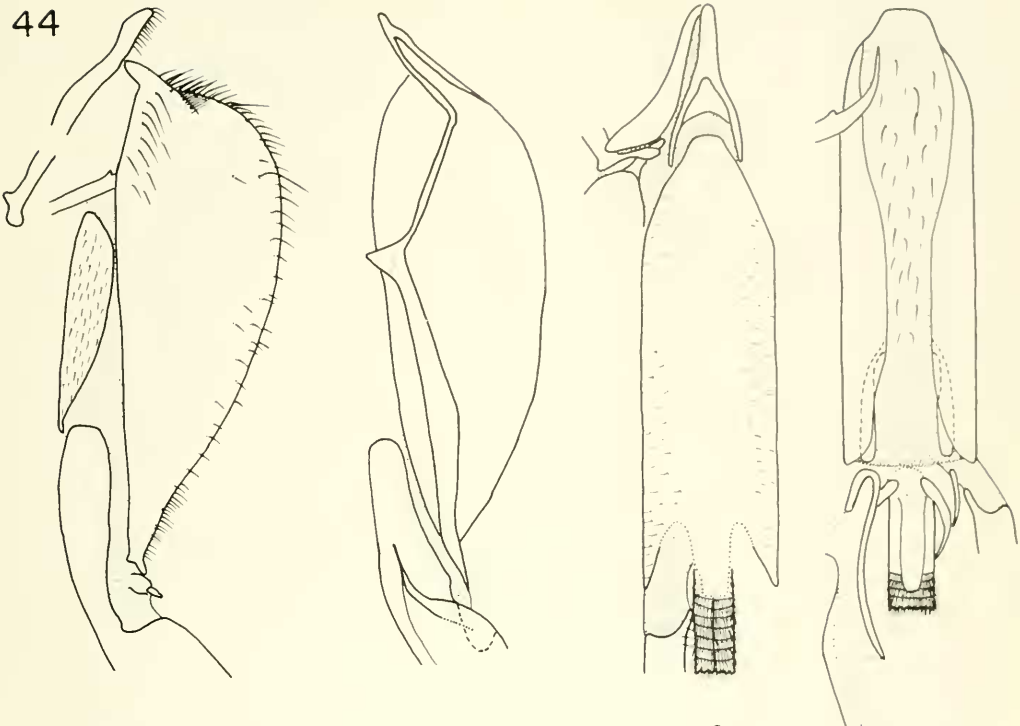

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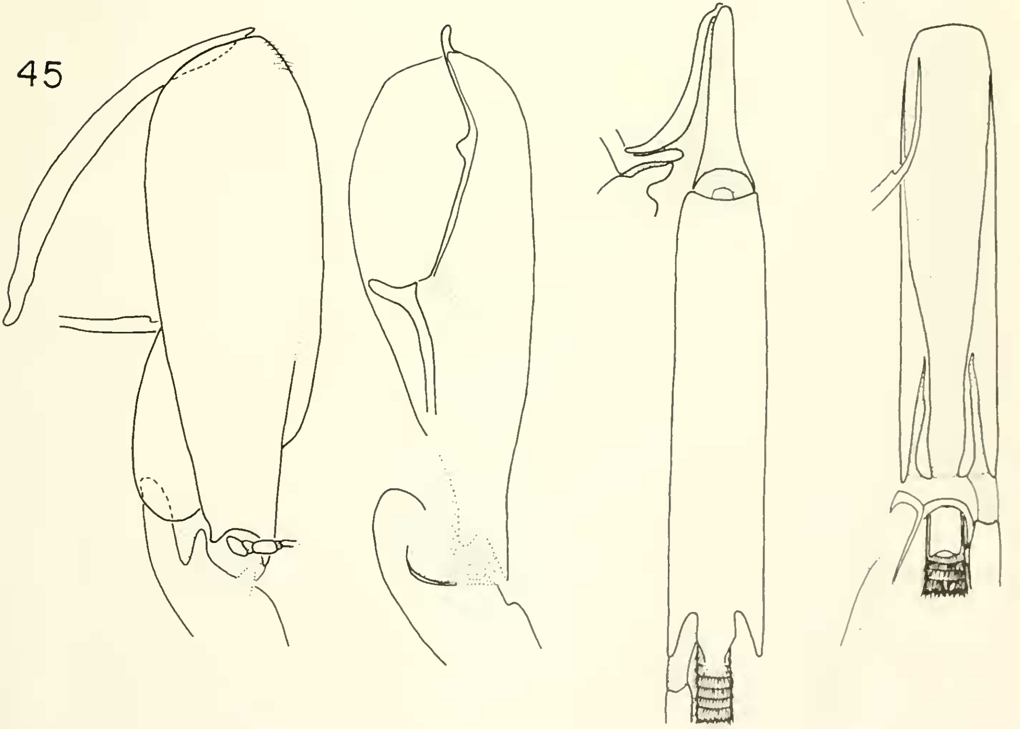

Fig. 44: *Mesocheira bicolor.*

Fig. 45: *Triepeolus verbesinae.*